Proceedings
-1953
V. 3A

B. C. F. I. LIBRARY
JUN 4 1959
FISH & WILDLIFE SERVICE

PROCEEDINGS

OF THE

EIGHTH PACIFIC SCIENCE CONGRESS

OF THE

PACIFIC SCIENCE ASSOCIATION

1953

VOLUME III A

OCEANOGRAPHY AND ZOOLOGY

Published by the
NATIONAL RESEARCH COUNCIL OF THE PHILIPPINES
UNIVERSITY OF THE PHILIPPINES
QUEZON CITY, PHILIPPINES
1957

PERIODICAL
Pacific
Science
Congress.
Proceed.
8th
1953
V.3A

~~DATE OF MAGAZINE~~	BORROWER'S NAME	TIME XXX out
3/11/76	moncrief	

PERIODICAL
8th
1953
Vol.3A

Pacific Science Congress, 8th
(1953).
Proceedings, Vol.3A

1957

P. O. F. I. LIBRARY
JUN 4 1959
FISH & WILDLIFE SERVICE

Digitized by the Internet Archive
in 2026

https://archive.org/details/proceedings-of-the-eight-pacific-science-congress-of-the_1953_3a

LIBRARY
BUR. OF COMM. FISH.
HON. BIOL. LAB.

PROCEEDINGS

OF THE

EIGHTH PACIFIC SCIENCE CONGRESS

OF THE

PACIFIC SCIENCE ASSOCIATION

Held at the University of the Philippines
Diliman, Quezon City
16th to 28th November 1953

UNDER THE AUSPICES
OF THE
NATIONAL RESEARCH COUNCIL OF THE PHILIPPINES
AND THE
REPUBLIC OF THE PHILIPPINES

VOLUME III A

OCEANOGRAPHY
AND ZOOLOGY

Published by the
NATIONAL RESEARCH COUNCIL OF THE PHILIPPINES
UNIVERSITY OF THE PHILIPPINES
QUEZON CITY, PHILIPPINES
1957

8th (1953)
V.3A
2261^60

Eighth Pacific Science Congress
and
Fourth Far-Eastern Prehistory Congress

COMMITTEE ON PUBLICATION AND DOCUMENTATION

Chairman: Dean Patrocinio Valenzuela
Co-Chairman: Prof. Gabriel A. Bernardo

Prof. H. Otley Beyer
Dr. Silverio M. Cendaña
Mrs. Araceli P. Gaffud
Mrs. Pilar A. Hallazgo
Mrs. Teresa V. Daza
Mrs. Luz B. Lardizabal
Prof. E. Arsenio Manuel
Mr. Teodoro G. Megia
Mrs. Rosario Mendoza
Dean Leopoldo B. Uichanco
Dr. Deogracias V. Villadolid

CONTENTS

VOLUME III A

OCEANOGRAPHY AND ZOOLOGY

PAGE

SYMPOSIUM ON POND FISH CULTURE

Proceedings 851
Opening Remarks. By Deogracias V. Villadolid 853
On the Ecology of Freshwater Fishponds in Indonesia. By K. F. Vaas 855
A Repressive Factor Controlling Reproduction in Fishes. By H. S. Swingle 865
Production Problems of Chanos Culture in the Philippines. By Deogracias V. Villadolid and Herminio R. Rabanal 873
Nursery Pond Management Techniques in Philippine Chanos Fishponds. By Herminio R. Rabanal and Heraclio R. Montalban 887

SYMPOSIUM ON ECOLOGY OF CORAL ATOLLS

Proceedings 903
Introduction to Special Symposium on Ecology of Coral Atolls. By Harold J. Coolidge 905
The Geology of Atolls. By Joshua I. Tracey, Jr. 907
Observations sur les Falaises et les Phosphates de Makatea (Ile des Tuamotu)—le Probleme de la Consolidation, des Sediments. Par Gilbert Ranson 909
The Hydrology of Atolls. By Ted Arnow 919
An Enumeration of the Hypothetical Roles of Algae in Coral Atolls. By Maxwell S. Doty 923
Factors Influencing the Distribution of Corals on the Reefs of Arno Atoll, Marshall Islands. By Robert W. Hiatt 929
Scarides et Milieu Corallien; Notes Biogeographiques. Par Théodore Monod 971
Observations sur les Facteurs Biologiques de la Dissolution du Calcaire D'origine Recifale dans les Tuamotu. Par Gilbert Ranson 979
Observations sur les Iles Basses des Tuamotu (Oceanie Française). Par Gilbert Ranson 989
Nature and Origin of Atolls (A Progress Report). By Preston E. Cloud, Jr. 1009
Soils, Vegetation and Agriculture on Coral Atolls. By F. R. Fosberg 1037
Relation of Humans to the Atoll Environment. By Alexander Spoehr 1049
Crustaces Decapodes Paguridae D'Oceanie Française. Par Jacques Forest 1053
Observations sur l'epoque de la Reproduction de *Pinctada margaritifera* (L.) et de Quelques Autres Organismes Marins dans les Tuamotu. La Cause du Namisme de *P. margaritifera* (L.) dans le Lagon de Takapoto. Par Gilbert Ranson 1077

PAGE

SYMPOSIUM ON PRODUCTIVITY IN TEMPERATE AND TROPICAL WATERS

Proceedings 1081
Fish Production in Fresh Water Units of Japan. By Katsuzo Kuronoma 1089
Herbivorous Animals and the Fertility of Tropical Inland Waters. By R. S. A. Beauchamp 1105
Some Considerations on Estuarine Productivity. By E. J. Ferguson Wood 1107
Some Aspects of Productivity in Relation to Fisheries of Indian Neritic Waters. By N. K. Panikkar and R. Jayaraman 1111
Factors for Fish Productivity. By A. G. Huntsman 1123
The Productivity of Temperate and Tropical Waters. By R. S. Wimpenny 1131
A Note on the Productivity of the Waters of the Northern Region of the Indian Ocean. By R. B. Seymour Sewell 1139
Phytoplankton Production in Relation to Depth and Distance in the Bay of Bengal off the Waltair Coast. By P. N. Ganapati and V. S. R. Murthy 1145
Some Chemical and Physical Factors Controlling the Biological Productivity of Temperate and Tropical Oceanic Waters. By L. H. N. Cooper 1157
The Influence of Turbulence and Vertical Exchanges on Plankton Production in the Sea. By T. J. Hart 1165
The Influence of Larval Settlement upon the Composition of Marine Level Bottom Communities. By Gunnar Thorson 1171
Present Status and Future Development of Oceanography. By Richard H. Fleming 1177

ZOOLOGY

Resolutions Adopted in the Eighth Pacific Science Congress Concerning Zoology 1197

Proceedings 1198

Proceedings 1199
Relationship of Entomology to Plant Quarantine. By David Miller .. 1205
Progress in the Control of Invertebrate Pests in the Pacific Islands. By C. E. Pemberton 1205
Control of Bee Diseases with Sulpha Drugs and Antibiotics. By H. Katznelson 1219
Biological Control of Noxious Insects and Weeds in Canada. By A. B. Baird 1227
An Annotated List of Infectious Diseases of Insects in Hawaii. By Yoshinori Tanada 1235
Some Features of the Insect Pests of the Rice Plant in Hokkaido, a Northern Limit of Rice Culture in Relation to Recent Developments in Culture Methods. By Satoru Kuwayama 1251

PAGE

Proceedings 1261
Observations on Behavior of Australian Thynninae. By B. B. Given 1265
Observations on the Biology of *Opius oophilus* Fullaway (Braconidae—Hymenoptera). By Frank H. Haramoto 1275
Occurrence and Nature of Explosive Outbreaks of Various Insect Pests in the Philippines. By Leopoldo B. Uichanco 1291
Sur les Parasites de l'*Elaeis* et de l'*Hevea* dans la Peninsule de Malacca. Par P. Vayssiere 1295
Further Studies on the Biology, Ecology and Control of the Black Beetle of Coconut *Oryctes rhinoceros* Linn. By Pedro Sison 1299
Rhinoceros Beetles as Pests of Coconut Palms. By J. Linsley Gressitt 1319
The Rhinoceros Beetle as a Regional Problem in the South Pacific. By L. J. Dumbleton 1325
Notes on *Oryctes rhinoceros* Linn. in Fiji. By B. A. O'Connor 1329
Small-Sample Techniques in the Analysis of Fruit Fly Population Phenomena. By Irwin M. Newell 1337
A Biological Study of *Bactrocera umbrosa* (Fabricius) (Trypetidae, Diptera). By S. M. Cendaña and P. P. Namocale 1347
Observations on the Rhinoceros Beetle *Oryctes rhinoceros* in Malaya. B. T. R. Gardner 1371
Sur les Caleopteras Lucanides des Philippines note sur leur Chorologie. Par E. Séguy 1375

Proceedings 1379
Insect Distribution and the Theory of Continental Drift. By E. B. Britton 1383
Remarques sur la Repartition des Scorpiones en Oceanie. Par Max Vachon 1393
Range-Changes and Differential Selection in Fruit-Pigeons of the *Ptilinopus purpuratus* Species-Group. By A. J. Cain 1393
Entomological and Plant Pest and Disease Control Work in the Philippines With Special Reference to That of the Bureau of Plant Industry on the Migratory Locust and Other Major Pests and Diseases of Crops. By Faustino Q. Otanes 1413
Further Studies on the Biology, Ecology and Control of the Giant East African Snail (*Achatina fulica* Fer.). By Guillermo A. Pangga .. 1433
The Insect Fauna of Micronesia. By J. Linsley Gressitt 1453
Status of Terrestrial Malacological Research in the Central Pacific and Micronesia. By Yoshio Kondo 1457
Land Molluscan Distribution in the Southwest Pacific. By A. W. B. Powell 1461
Status of Tamaraw, *Anoa mindorensis* (Heude). By Canuto G. Manuel 1463
Collection and Distribution of Beneficial Insects in the Pacific Area and Southeast Asia. By T. R. Gardner 1475
The Distribution of Terrestrial Reptiles in the Islands of the Pacific Basin. By Walter C. Brown 1479

Proceedings 1493

PAGE

Report of the Standing Committee on Systematic Zoology. By H. Boschma 1495
Arthropod-borne Parasites of the Domestic Animals in the Philippines. By L. M. Yutuc 1511
The Insect Fauna of the Ryukyu Islands. By J. Linsley Gressitt 1533
Hispine Beetles of the Coconut Palm. By J. Linsley Gressitt 1539
Some Mimicry Patterns of Philippine Insects. By Henry Townes 1546
Parasites of Tent Caterpillars (Lepidoptera: Lasiocampidae) in the Lower Fraser Valley of British Columbia, Canada. By J. H. McCleod and G. L. Ayre 1547
European Agriotes Wireworms (Elateridae) Found Established in Coastal British Columbia, Canada. By K. M. King and A. T. S. Wilkinson 1561
Three Fruit Flies (Tephritidae) of Economic Importance in Hawaii. By Henry A. Bess and Toshiyuki Nishida 1562
Spiders in Samoa and the Southwest Pacific. By B. J. Marples 1573
Marine Wood-boring Mollusca of the Philippines. By Robert C. Miller 1575
Spider Predators of the Spruce Budworm, *Choristoneura fumiferana* (Clem.) at Lillooet, B. C., Canada. By A. L. Turnbull 1579
The Guitarfishes, Family Rhinobatidae, of the Philippines and Adjacent Seas. By Albert W. C. T. Herre 1595
Population Studies and Some Aspects of the Ecology of Potato Aphids in Selected Areas in Canterbury, New Zealand. By B. B. Watts .. 1621

November 23, 1953

SYMPOSIUM ON PONDFISH CULTURE

Convener: Dr. Deogracias V. Villadolid, Director, Bureau of Fisheries, Manila.

Secretary: Mr. Pedro A. Acosta, Bureau of Fisheries, Manila.

PROCEEDINGS

Dagatdagatan Saltwater Fishery Experimental Station
Malabon, Rizal

The symposium convened at 0900 hours. Dr. Villadolid * spoke briefly on the manner in which the symposium was to be conducted, the number of minutes to be alloted to each paper and the scope of the discussion. He also spoke on the establishment of the station, the important role it has played on the fishpond industry and on the importance of pondfish culture to the Philippines.

After his introductory remarks, the convener called on Dr. Hardenberg to read Dr. K. F. Vaas' paper "On the Ecology of Freshwater Fishponds in Indonesia."

Discussion

Manacop: Upon what does tilapia subsist mainly?

Hardenberg: Tilapia feeds largely on algae. Because of this fact this species has been utilized largely in cleaning ponds of algae and other aquatic vegetation floating on the water, which serves as breeding places of malarial mosquitoes in Indonesia.

Mr. H. W. Swingle's "A Repressive Factor Controlling Reproduction in Fishes" was not read by him but was presented orally with the aid of a flannel board as his illustration.

Discussion

Hiyama: This question is not related to the subject matter. May I know what makes these figures made of cardboard stick to the flannel board?

Swingle: It's simple. Sandpaper is pasted behind these figures so that they readily attach or stick on the flannel.

Halstead: What can this repressive factor be?

---

* See page 853 for the introductory remarks.

SWINGLE: It's a hormone-like excretion or secretion in fishes, the identity of which is still unknown.

HALSTEAD: I presume that it is due mainly to some endocrine secretion which must be studied thoroughly. After this discussion recess for refreshment was announced by Dr. Villadolid.

The session was resumed at 1130 hours with Mr. Rabanal presenting "Production Problems of Chanos Culture in the Philippines" by Dr. D. V. Villadolid and H. R. Rabanal. He classified the problems into two categories. First, those bearing directly on the loss or mortality of Chanos under cultivation, and second, those dealing with fishpond pest and nuisances which tend to increase the cost of production. With aid of diagrams he discussed in detail the various problems under each category.

(There was no discussion)

Mr. Rabanal again presented "Nursery Pond Management Techniques in Philippine Chanos Fishponds" by H. R. Rabanal and Heraclio R. Montalban. He divided the culture of Chanos in the Philippines under three stages namely: (1) the rearing of fry and fingerlings in the nursery ponds, (2) the growing and stunting of fingerlings in the transition pond and (3) the raising of fingerlings to marketable sizes in the rearing pond. Mr. Rabanal stressed the fact that the rearing of fry and fingerlings in the nursery is the most important of the three stages because upon this depends the success of the next two stages. He discussed in detail the various nursery pond management techniques such as cultivation and leveling of pond bottom, water management to effect growth of the desirable fish food organisms, stocking rate and stocking procedure, etc.

There being no discussion, the morning session was declared closed about 1330 hours. Lunch was served followed by a short musical program wherein native folk dances were performed by personnel of the Bureau of Fisheries. After this program the afternoon session was resumed at 1600 hours. Colored slides depicting various important activities involved in bañgos culture such as preparation of the nurseries, transplantation of fingerlings, planting of algae, etc., were shown with Mr. Rabanal giving commentaries. Dr. Villadolid expressed his thanks for the splendid cooperation and attendance of the delegation as well as non-delegates present during the symposium.

OPENING REMARKS

By Deogracias V. Villadolid

Ladies and Gentlemen, Co-workers and Friends:

Where we are now today stands the monument of my country's pioneers in fish culture who had the foresight to see the nation's potentialities in brackish and fresh-water fishery resources. This fishery experimental station was conceived in 1934 to begin an inquiry into the technical requirements of how to harness these resources. Fish culture in the Philippines, principally of *Chanos chanos* dates back centuries ago but its progress was slow due to the dearth of scientific knowledge and information on the technical requirements of fish pond management. The slow progress was also due, to a large measure, to one or two factors, namely: the production of the planktonic and algal food of the culture fish and the lack of financial system by which fish pond areas may be enlarged in a much quicker pace from the undeveloped swamplands and bayous.

Out of the 600,000 hectares of swamplands there are at present only 88,000 hectares of developed ponds involving an investment of approximately ₱176,000,000.00 or 88 million U.S. dollars, and the employment of no less than a hundred thousand people. The estimated yearly production of these fishponds is 31 million kilograms of fish valued at ₱46,000,000.00. I need not state that if the area of these fishponds is increased to at least one half of the available swamplands, which is 300,000 hectares, the production of *Chanos chanos* and other cultivable species of fish in fishponds would be increased to six times 31 million kilograms or 186 million kilograms of fish a year. Considering also the fact that through improved methods and techniques of planktonic and algal production, the annual target production of 300,000 hectares of fishponds in the Philippines will be somewhere approaching 300,000,000 kilograms or 300,000 tons a year. Hand in hand with these efforts of the Bureau of Fisheries in the rational exploitation of fishpond resources is the recent enthusiasm on the part of our government to extend a financial system of loaning to fishpond operators money at the rate of ₱800.00 a hectare for a maximum area of 25 hectares.

I am particularly overjoyed, not to say, inspired, on the occasion of this symposium on pondfish culture in this very place established for the purpose of improving on the Philippine's technique in fish culture, because of the presence here of experts from whom we expect guidance on the very important problems we wish to solve in our bid to achieve self-sufficiency in fish protein. In 1948, I tried to contact an outstanding authority on this subject in the United States. Unfortunately, due to wrong timing of travel I was deprived of the opportunity to meet him. Fortunately, however, the Eighth Pacific Science Congress has presented the chance to enable me to bring the "mountain to Mohammed instead of Mohammed to the mountain." And here I am face to face with the same outstanding authority on how to raise more food in fishponds to increase production of culture fish. For as I have said, our most difficult problem is to increase fish production in ponds without undergoing high overhead expenses in the construction of large areas of ponds. Dr. Homer S. Swingle, permit me to announce with pride and pleasure to state that the outstanding authority on this subject I was alluding to is no other than your good self.

The paper on "Production Problems of *Chanos chanos* in the Philippines" is to be presented by my co-author, Mr. Herminio R. Rabanal, in a brief and concise manner so that it will leave plenty of time for answering questions that may arise from the public. The paper will be followed by the other paper to be presented by Mr. Rabanal on an allied subject. I have requested a panel of Philippine consultants on our fish culture in the Philippines to be with us here today so that they may also be ready to answer questions which may be referred to them. The paper of Dr. Vaas on "The Ecology of Freshwater Fishponds in Indonesia" is to be presented by Dr. Hardenberg and the paper of Dr. Swingle entitled "A Repressive Factor Controlling Reproduction in Fishes," which will be presented by the author, himself, will be given adequate time for presentation and discussion. During the lunch hour the Bureau of Fisheries is presenting an entertainment program for the benefit of our distinguished visitors.

ON THE ECOLOGY OF FRESHWATER FISHPONDS IN INDONESIA

By K. F. Vaas
Laboratory of Inland Fisheries, Bogor, Indonesia

Introduction

Indonesian fishponds can be divided into three groups:

1. Brackish water ponds along the shallow sea coast, where *Chanos chanos* (Forsk.), *Tilapia mossambica* Peters, and various prawns are grown;

2. Paddy-fields, where various forms of pisciculture, notably with the common carp are practised;

3. Freshwater ponds, where various Cyprinidae and Labyrinthici are cultivated, sometimes as monocultures and more often mixed.

In the present article an attempt will be made to consider the ponds of the third group from an ecological point of view.

The first category was described in detail by Schuster (1949) while the author, in collaboration with M. Sachlan, gave a description of the most important biota involved. (Vaas and Sachlan 1952). The ecology of the Hawaiian Chanos-pond was described by Hiatt (1944).

This group of ponds is characterised by a marked uniformity, lacking in the other groups, a result of the fact that the water feeding the ponds is mainly seawater and the principal fish cultivated is a single species, viz. the Chanos. The factor soil is the most variable one, and the work of Markus (1941), carried out in Indonesia, is a first attempt to understand its influence.

The paddy-fields have in common with the brackish-water ponds the extremely limited number of fish-species cultivated, but here the factor water is as variable as the factor soil. At the moment insufficient data on the biota of Indonesian paddy-fields have been assembled (*vide* Bernard 1908, 1908, Van Oye 1921, 1922, Vaas 1947). This is the reason why no adequate ecological classification of sawah-fish ponds can be made and the present article is limited to freshwater ponds.

For the paddy-fields in Krian (Malaya), cultivated with *Trichogaster pectoralis* (Regan), Soong (1952) described some interesting relationships between the fertility of the soil, the yield of the fish and the occurrence of various micro-organisms.

ENVIRONMENTAL FACTORS

Various environmental factors have already been mentioned in the introduction. They might be divided into a group of external factors, influencing the eco-system from the outside, and a group of internal factors.

Within the first group the factors: sun, rain, air, inflowing and outflowing water, and, last but not least, man—in casu the fishfarmer—should be distinguished.

The second group comprises the factors: soil, water, biota other than fish, and fish.

Among the factors of the first group, sun, rain and water-supply are active, in one direction only i.e., they affect the eco-system but are not affected themselves, thus, there is no interaction between them and the pond. Moreover, with reference to sun and rain there is but little that can be done by the farmer, except in a negative way by shading the pond.

The heat and light of the sun exerts an influence on nearly all units of the system. Sunlight dries out the soil, heats the water and influences its capacity for holding gases in solution, provides the chlorophyl-bearing plants and photosynthetic bacteria with energy, inhibits various other bacteria, and regulates the metabolic rate of all poikilothermic animals—notably fish—via the temperature of the water, as well as the respiratory activity of plants and bacteria.

A second factor, also "straight from Heaven," is the rain, which affects the soil, and, more in particular, the water, where it, usually, lowers the temperature and occasionally, increases the turbidity, thus decreasing the photosynthesis of the submerged vegetation to a marked extent (*vide* Meyer and Heritage 1941, difference between photosynthesis of Coratophyllum in clear and turbid water). The rain usually decreases the concentration of the dissolved minerals while it increases the oxygen content and, often, the amount of nitrogenous substances (thunderstorms). (*Vide* Vaas 1952).

Between the air and the eco-system of the pond many interactions can be pointed out, e.g., the exchange of heat between the air and both soil and water, and the exchange of gases dissolved in the water.

As to the water-supply, this factor is, contrary to the factors mentioned so far, highly controllable. The quantity of water can be regulated at will, and its quality can be adjusted by the addition of manure and fertilizers.

The second group, the internal factors, are characterised by the numerous, intricate interactions between soil, water, biota and fish. In fact, it might be held that the entire science of limnology aims at nothing else but the elucidation of these interactions.

Summarizing, the following picture might be drawn. The climate and the chemical and physical properties of the pond-soil and the water, together with the totality of cultural practices carried out by the fish-farmer, form the basic characteristics of the environment. Nature reacts on a given set of conditions by establishing the most adapted flora and fauna. According to their different abilities they will adapt themselves to the seasonal, diurnal and other changes in the environment, while competing with each other, sometimes helping, sometimes ousting one another, occasionally even exerting a considerable influence on the quality of the environment itself. (Interception of light by water-bloom, precipitation of calcium by algae, secretion of lethal toxines by flagellates, increase of turbidity by carps, etc.)

Since it is the ultimate aim of the fishfarmer to provide his fish with an environment that is most suitable, the specific requirements of the species of fish cultivated in freshwater ponds should receive our attention in the first place. These requirements pertain to feeding and spawning. Feeding is a continuous process, whereas spawning is an incidental one only. For spawning, usually, special techniques are resorted to, while the process of spawning the fish is often carried out in special ponds. The best way of classifying Indonesian freshwater fish ponds will be to inquire how they fulfill the feeding requirements of the fish.

In ponds fish may subsist either on natural food—the organisms growing in the pond as a result of its own fertility as well as through the addition of manures and fertilizers etc.—or on fodder, added by the farmer as a special meal for the fish. It has repeatedly been shown that even the best kinds of fodder cannot be used as sole food for fish; a large percentage of natural food should always be present. In Indonesia bran is about the only kind of fodder added, while, in most cases, part of it is not directly ingested but drops to the bottom of the pond, where it acts as a manure. The production of natural food is, therefore, the most important problem and in the present article some examples will be given of biota living in various types of freshwater ponds, while their relationships to physical and chemical properties of those ponds will be described. Furthermore, some cultural methods utilized to propagate those organisms, which will meet the feeding requirements of the cultivated fish in the best way, will be discussed.

Description of Various Types of Ponds

In Indonesia, notably in Java, freshwater ponds are found wherever sufficient water is available, i.e., they are excavated in soils ranging in fertility from rich to poor and are fed with water ranging in mineral content, particularly lime, from high to low.

In many places also paddy-fields are used for fishculture, either after harvesting the rice or while the rice is still on the field. In the latter case the fish—notably common carp—will swim amidst the rice plants.

Since Java is a densely populated island with a heavy rainfall, running water is the usual means of discarding waste products of whatever kind. The fishfarmer has learned to use these wastes to enrich his pond. Many ponds in the immediate vicinity of villages and towns are fed with water which might be called diluted sewage.

The most important fishes cultivated are the following:

1. *Cyprinus carpio* L.—common carp;
2. *Tilapia mossambica* Peters—ikan mudjair;
3. *Osteochilus hasselti* (C.V.)—nilem;
4. *Puntius javanicus* (Blkr.)—tawes;
5. *Holostoma temmincki* C.V.—tambakan. *Trichogastor trichopterus* (Pall.)—sepat siam, and *Osphronemus goramy* Lac.—gouramy, are not of sufficient importance to be inserted in a general survey as is intended here.

The food requirements of these fish are listed below in Table I.

TABLE I

Food Requirements of the Principal Fishes Cultivated in Freshwater Ponds in Indonesia

Species	Submerged Higher Plants	Thread Algae	Periphyton	Phytoplankton	Crustaceans Zooplankton	Insects and Larvae	Worms
1. Common carp		xx	x	x	xxx	xxx	xxx
2. Tambakan		x	xx	xxx	xx		
3. Mudjair	x	xx	xxx	xxx	x		
4. Nilem	xx	xx	xxx	xxx	x		
5. Tawes	xxx	xx	xx	xx			

In this table the main food is indicated by three crosses, accessory food by two, and emergency food by a single cross. Carp is a bottom-feeder, tawes a vegetable-feeder, tambakan a plankton-feeder, nilem a periphyton-feeder and mudjair subsists on periphyton, plankton and thread algae.

But for carp, grown in paddy-fields, monocultures are exceptions and mixed crops are the usual practice. The differences in the diet of the species mentioned explain why various combinations will be successful, especially since tawes, though showing a distinct preference for soft submerged higher plants (Hydrilla) in natural waters, will grow well, feeding on a mixture of thread algae and periphyton, in ponds.

All groups of biota mentioned in Table I are far too complex to have their environmental requirements as a group stated. Besides generally, even for a single species or organism too little is known to be able to encourage and propagate them at will. In this respect the work of Rhode (1948–'50) and Osterlind (1948–'50) is referred to.

Many data referring to the physical and chemical properties of the water of Indian ponds and the composition of the existing biota are published in the annual reports of the various Fisheries Departments, e.g., the Progress Report of the Madras Rural Piscicultural Scheme, April 1950–March 1951. (S. V. Ganapati, P. I. Chacko, B. Krishnamurti, and others.)

Gonzalves and Joshi (1946) studied seasonal succession of algae in ponds and found, e.g., that Cyanophyceae require a high concentration of dissolved minerals and organic matter. Euglena does not require such a high mineral content but subsists on organic substances while it does need a high temperature.

Mookerjee and Bhattacharya (1949) studied the cycle: $Ca(HCO_3)_2$ + dissolved organic matter → Cyanophyceae + Crustaceans → carps. They found that rain caused a decrease in the fish production via a decrease in both the preceding links in the chain, whereas manuring with either dung or decomposed plant parts effected an increase for the opposite reason.

A notable contribution is the recent work of Komarovsky (1952) on the biota of Israelian carp-ponds.

In the case of Indonesian ponds a clear distinction can be made between: ponds with a heavy submerged vegetation and adherent periphyton; those with a pronounced development of plankton; and those with a strongly developed bottom fauna. In the first group of ponds the nilem is the principal species grown, in the second one the tambakan and in the third group the carp.

There are numerous indications in limnological literature that a heavy growth of submerged higher plants is never combined with a strong development of phytoplankton, due to their competition for minerals, and especially for sunlight. A water-bloom of plankton absorbs too much light, thus, the sunlight on the bottom will be insufficient for the juvenile stages of the higher plants which must begin their development here. (Swingle 1947, Vaas 1952.)

Accordingly, the typical nilem-ponds of West-Java are densely overgrown with *Hydrilla verticellata* (L.f.) Royle, *Ceratophyllum submersum* L. and *C. demersum* L., and *Najas falciculata* A. Br., with enormous numbers of epiphytic diatoms (Navicula, Gomphonema, and notably, Cocconcis), small hormogenic blue-green algae and green thread algae. Phytoplankton is poorly developed in the clear, transparent water.

A heavy photosynthesis creates a saturation—often even a supersaturation—of dissolved oxygen and a CO_2-deficiency in the daytime. The nilem, originally a river fish, needs a high oxygen tension and cannot be cultivated in turbid water with an oxygen-deficiency. Since the buffer-capacity of the majority of these ponds is rather high, an accumulation of CO_2 during the night need not be feared. Frequently, such ponds do not receive any manure, especially when the water is fertile. An example of such a pond is given in No. 1 of Table II.

With the purport of utilizing the natural food not taken by the nilem, carps are often stocked in the same ponds. In the case of the pond described as No. 2 in Table II, the natural fertility had been increased by the addition of nightsoil as well as bran, on account of the rather heavy mixed crop of nilem and carp. As a result, various Protococcales, such as Scenedesmus, Pandorina, Eudorina and Pediastrum increased in number.

On the other hand, there is the group of ponds stocked with tambakan, mudjair and tawes, or mixtures of these three species. In this case a well-developed plankton is aimed at. Examples of such ponds are No's 3, 4, 5, and 6 of Table II. The acidity of the water is determined by the calcium content of the water, together with the CO_2-production of the decomposing kitchen-waste, green manure and other kinds of organic matter.

Free CO_2 is always present. Dissolved organic substances are often present in high concentrations while the oxygen tension during daytime is frequently below the saturation point. Cyanophyceae (Oscillatoria, Microcystus), diatoms (Navicula, Gomphonema, Melosira, Synedra), green algae, such as Pandorina, Eudorina and Scenedesmus, Flagellates (Euglena, Phacus), Crustaceans (Cyclops, Bosmina, Diaphanosoma) and Rotifera (Brachionus, Polyanthra, Filina, Keratella) abound in the water. Some Oligochaetes and Tentipedidae (Chironomus larvae) are often found in the mud on the bottom. Submerged higher plants are usually absent. On poor soils the pH can be as low as 6–6.5 (pond No. 3). Heavy manuring may, sometimes, lower the pH of ponds with a fair calcium-content (pond No. 4). The age-old practice of stirring the water with rods is occasionally used in these ponds (No. 4) as a typical means of fertilizing the water and not the soil, thus encouraging the plankton and not the rooted vegetation. (*vide* Vaas 1952).

The common practice in carp-ponds, where carp is often mixed with tawes and tambakan, is a heavy manuring with human excrements or sewage. CO_2-production and oxygen-absorption is high on the bottom, and, as is shown by example No's 7 and 8 in Table II, even at the surface the dissolved oxygen does not reach the saturation-point. As is demonstrated by example No. 9 there is, in many cases, a large difference between the oxygen tension at the surface and on the bottom, although the pond at Bandung, used in this example, was nowhere deeper than 60 cm.

Zooplankton, together with Diatoms, Protococcales and, often, Cyanophyceae are abundant in the water. The surface is often entirely covered with an F brownish-red film of *Euglena sanguinea* Ehr., (No's 9 and 10). These red films are composed of cysts of Euglena, containing an increased quantity of haematochrome. When these flagellates are dividing vigorously, they are highly motile, the amount of haematocrome is less and film is green.

The pond produces many Temtipedides and Oligochaetae (Dero, Aulophorus, Nais, Pristina and Chaetogaster) feeding on detritus, derived from the dead plankton, vegetable débris and other organic matter, on the bottom of the pond. These organisms are eagerly sought and eaten by the carps. The carps themselves are constantly grubbing in the bottom and raking up a lot of mud. Thus, they add to the turbidity of the water.

An extreme case is given in example 2 of Table II, where conditions are described as found in an open sewer, running through a densely populated area of the city of Bandung, where common carp are cultivated in bambu cages, suspended in a constant flow of heavily polluted sewage. Practically no organisms are found in the water itself. On the bambu strips of the cages are found: Cyanophyceae, *Zoogloea ramigera* Itz., Sphaerotilus and Beggiatoa, while an outburst of Oligochaetae and Tentipedidae occurs on the sand, mud and small gravel of the bottom of the sewer. These organisms were found in enormous quantities in the guts of the carps. As seen in the table, the oxygen tension is low, in fact, it is too low to grow a species other than the common carp.

Another interesting case of carp-culture, based on the addition of human faeces into open sewers, was studied by M. Sachlan in ponds near Jogjakarta. Although most data were, unfortunately, lost during the war, the following outline might be presented.

These ponds were fed with water from a sewer, straight from the city-drains, mixed with ordinary irrigation-water from the neighboring paddy-fields. When the amount of faecal matter became too large, the inflowing water could be led past the ponds; and this was necessary because the water would have obtained a black colour and a strong faecal smell, even after mixing with normal water. In these cases no oxygen would be found in it. When the sluices to the first pond are not closed early enough, a heavy mortality rate will be the result. The inflowing water from pond No. 1 flows into pond No. 2, and so on.

In the first pond only bottom-dwelling Cyanophyceae were found and hardly anything else. Strong photosynthesis at noon may buoy up patches of threads, seen floating on the surface. In the morning oxygen-tensions of about 30% saturation were observed.

In the second pond Euglena covers the surface entirely and zooplankton abounds in its water. The amount of light is insufficient for phytoplankton.

In the ponds further down were found water-blooms of Anabaena.

It must be borne in mind that even though the use of human excreta is a widespread practice in Indonesia, albeit not in such a pronounced form as in the examples mentioned above, it, apparently, never gave rise to complaints connected with infectious diseases, from the consumers of the fish. Just how quickly and thoroughly a fishpond is able to extinguish pathogenic bacteria, might be estimated from the results of Schaeffer's investigations in a sewage pond at Jogjakarta (Schaeffer 1940, *vide* also Vaas 1948).

ACKNOWLEDGMENT

The author is greatly indebted to M. Sachlan (Laboratory of Inland Fisheries, Bogor) and Mrs. A. Vaas-Van Oven (Agricultural Senior Highschool, Bogor) for valuable advice and the use of unpublished data, and to R. Odjoh Ardiwinata, who was the first to show him the Tasikmalaja pond-area.

LITERATURE

BERNARD, C. Protococcacees et Desmidiacees d'eau douce recoltees a Java. Batavia. (1908).

——— Sur quelques algues unicollulaires d'eau douce. Buitenzorg. (1909).

GONZALVES, E. A. and D. B. JOSHI. The seasonal succession in a tank at Bandra. *Journ. Bombay Nat. Hist. Soc.* 46 (1946): 154.

HIATT, R. W. Food-chains and the food-cycle in Hawaiian fishponds I and II. *Trans. Am. Fish. Soc.* 74 (1944): 250 and 260.

KOMAROVSKY, B. A comparative examination of the relationship between the "limiting elements" and the development of phyto-plankton in several types of artificial fish-ponds. *Bamidgeh.* 4(1952): 137.

MARKUS, B. Over de slibbodem van zoutwatervijvers. Verslag van de 28ste Vergadering van de Vereniging voor Proefstations personoel to Buitenzorg. *Landbouw.* 17(1941): 891.

MEYER, B. and A. HERITAGE. Effect of turbidity and depths on apparent photosynthesis in Coratophyllum. *Ecology.* 22(1941): 17.

MOOKERJEE, H. K. and R. N. BHATTACHARYA. Culture of fish in temporary hard waters. *Proc. of the Zool. Soc. of Bengal.* 2(1949): 164.

OSTERLIND, S. Growth conditions of the alga *Scenedesmus quadricauda*, *Symbolae Botanicae Upsaliensis.* 10/3 (1948-'50).

OYE, P. VAN. Iets over de microflora on fauna der rijst velden. *Natuurkundig Tijdschrift.* (Vlaanderon) 3(1921): 121.

———— Contribution a la connaissance de la flora et de fauna microscopique des Indes neerlandaise. *Ann. de Biol. lacustre.* 11(1922): 130.

RHODE, W. Environmental requirements of freshwater plankton. *Symbolae Botanicae Upsaliensis.* 10/1 (1948-'50).

SCHAEFFER, C. O. Onderzook naar het voorkomen van typhusbacterien in het rioolwater van Jogjakarta en hun gedrag tijdens de bezinking en de biologische reiniging. *Med. Dienst Volksgezondheid Ned. Indie.* 29(1940): 49.

SCHUSTER, W. H. Fishculture in saltwater ponds in Java. Bandung (1949).

SOONG, M. K. The fitness of ecological niches into which fish are introduced at various ages and the survival of the transplanted fish. *Proc. Indo. Pac. Fish. Council.* 3rd Meeting. Madras. Sect. II-III. (1952): 218.

SWINGLE, H. S. Experiments on pond fertilization. *Agric. Exp. Station of the Alabama Polytechnical Institute. Bull.* 264 (1947).

VAAS, K. F. Biologische inventarisatie van de binnenvisserij in Indonesie. *Landbouw.* 19(1947): 522.

———— Over het gebruik van visvijvers bij de reiniging van afvalwater in de tropen. *Landbouw.* 20(1948): 331.

———— Notes on, and possibilities of, fertilization of fishponds in Indonesia. *Proc. Nat. Inst. of Sc. of India.* 18(1952): 1.

———— and M. SACHLAN. Inventory of organisms in brackish-water ponds near Djakarta, with special reference to the plankton. *I.P.F.C. Special Publication* no. 2 (1952): 56.

TABLE II

SURVEY OF FRESHWATER FISHPONDS IN INDONESIA

LOCALITY	TASIK-MALAJA	TJIPANAS	AWIPARI (paddy fields)	TASIK-MALAJA	TASIK-MALAJA	INDIHIANG	TASIK-MALAJA	JOG-JAKARTA	BANDUNG	TJISAAT	BANDUNG (sewer)
Cyanophyceae	xxx	xxx	x	x	xx	x	xxx	x	xxx	x	xxx
Planktonic diatoms	xx	xx	xx	xxx	x	x	x	xxx		x	
Epiphytic diatoms	xxx	xxx									
Phyto-flagellates			xxx	xxx		x	xx	xx	xxx	xxx	x
Proto-coccales	xxx	x	xx	xx	xxx	xx	xxx	xxx	xxx	xxx	x
Green thread algae	x					x	x	xx	xx		xx
Crustaceans	xxx	x	x	xx	xx	xxx	xx	xxx	xx	xxx	
Rotifera	xx	x	xx	xx	xx	xx	xx	xxx	xx	xxx	x
Tenti-pedides			xx	xx	x	x	xx	xx	xxx	xx	xxx
Oligo-chaetes		x	xx	xx	x	x	x	xx	xx	xx	xxx
Fish [1]	N.C.	N.C.G.	T.	T.	Tw.	M.	C.T.N. G.	C.T.w. T.	C.M.	C.M. Tw.	C.
Turbidity + Colour	clear	clear	green	green	green	brown	turbid	green	turbid sewage	turbid	turbid
Manure	latrine	—	leaves	stable	leaves	—	leaves latrine	city sewage	—	stable	sewage
Fodder	bran	—	bran	bran	bran	bran	bran	—	—	bran	—
Submerged vegetation	heavy	heavy	—	—	—	—	—	—	—	—	—
pH	8,0–8,3	8,7	6,5–6,7	7,1–7,3	7,2	7,3–8,1	7,3–7,6	8,7	8,5	7,2–7,7	7,4–7,5
CO_2 mgr/1	def.	def.	50	20	15	13–0	40–10	def.	def.	10–9	9
Acidity [2]	1,3–2,3	2,4	1,3–1,5	2,3–2,4	1,3	1,3–1,8	2,3–2,8	1,8	2–2,5	1,1	
P mgr/1	0,004	0,035	0,02			0,0085	0,04				
NO_3 mgr/1	23	12	01		0	02					8
$KMnO_4$ mgr/1	27	24	45		14	66				20	46
SiO_2 mgr/1	27	4	9		22	22					114
O_2% Sat.	$100 \geq 100$	$100 \geq 100$	<100	(4)	<100	<100	80	>100–50		95–60	50–30
No.	(1)	(2)	(3)	<100	(5)	(6)	(7)	(8)	(9)	(10)	(11)

---

[1] C—Common carp; T tambakan; Tw—tawes; N—nilem; M—mudjair; G—gouramy.

[2] cco, 1*N* HCl on 200 cc. against methylorange.

A REPRESSIVE FACTOR CONTROLLING REPRODUCTION IN FISHES

By H. S. Swingle
Agricultural Experiment Station
Alabama Polytechnic Institute
Auburn, Alabama, U.S.A.

The various factors affecting reproduction of fishes have received inadequate attention when the importance of this knowledge is considered. For pond fish culture especially, there is need for information enabling the fish culturist both to induce and to prevent spawning by various species.

Experiments have been conducted for the past 19 years on production of various species of pond fishes at the Agricultural Experiment Station of the Alabama Polytechnic Institute in a series of 150 experimental ponds. In the course of this work, various factors affecting the reproduction of bluegills and bass have been investigated (Swingle & Smith, 1943). In recent years, work with goldfish, *Carassius auratus* (Lin.), with buffalo fish, *Megastomatobus cyprinella* (Val.), and the common carp, *Cyprinis carpio* Lin., and certain other fishes have indicated the presence of a hormone-like excretion or secretion from fish that acts as a repressive factor inhibiting reproduction in ponds. The experiments with various species indicating the existence of this repressive factor are given in this paper.

EXPERIMENTS WITH GOLDFISH

Experiments with goldfish were begun in 1932. In early experiments it was found that if ponds were stocked in January with a few goldfish (up to 200 averaging 4 ounces each) per acre, heavy reproduction resulted in February and March, while if large numbers (2000 or more averaging 4 ounces or larger) were stocked at this time little or no reproduction resulted.

This was originally thought to be due to the goldfish eating their own eggs. However, examination of the fish at the heavier rate of stocking indicated that eggs were well formed, but were never laid.

Also in the ponds with the lighter rate of stocking, egg-laying occurred in February and March, and then ceased. Examination of the adult fish demonstrated that the females contained well-developed eggs and the males ripe sperm throughout most of the summer. Transfer of these brood fish to new ponds freshly filled with water in July and August resulted in spawning within 48 hours.

These experiences indicated that something connected with density of population of goldfish was effective in preventing reproduction. It was evident from the above experiments that reproduction failed to occur or ceased where a considerable number or weight of either young or old goldfish were present. This suggested that the effect was possibly due to a "space factor."

However, additional experimentation indicated that this was not the case. In one experiment, goldfish were kept in a 0.1-acre wintering pond at the rate of approximately 3000 pounds of brood goldfish per acre. Under these conditions, no spawning had occurred by April, approximately 40 days later than the normal spawning period. The pond was drained, and all brood fish were concentrated in several holding tanks approximately 2 feet deep, 3 feet wide and 15 feet long. Fresh water from a stream that contained no goldfish was sprayed over the fish to keep them in good condition. Heavy spawning occurred in the tanks the next morning. This indicated that the "space factor" had nothing to do with the goldfishes' inability to spawn while in the wintering pond since they were much more crowded in the tanks. The same results were obtained in a later experiment. These results indicated that the repressive factor was something present in the water in which goldfish had been held for several months prior to their spawning period.

Upon the basis of these experiences, it was postulated that the repressive factor was a secretion or excretion from the goldfish themselves that exerted a hormone-like repressive effect upon maturing of eggs or at least prevented egg-laying. The fact that laying of viable eggs can often result within 24 hours after transfer of the brood fish to fresh water which had not previously contained goldfish, indicated that the eggs and sperms of the brood fish were practically mature, but the stimulus to egg-laying was repressed.

An additional series of experiments appeared to confirm the above theory. Two ponds were stocked with goldfish eggs on May 5, 1952, and were drained the following August 6. At that time they contained 779 and 516 pounds of goldfish per acre. Prior to removal of the goldfish, the water from these ponds containing goldfish was pumped into two new ponds that had previously remained dry. One pond was completely filled and the other was one-third filled with this water during the period August 1–6. At the same time, three other new ponds were filled with fresh water from a stream that did not contain goldfish. All ponds were stocked with brood goldfish taken from the same holding pond on August 6 to 8.

Heavy egg-laying occurred promptly in the three ponds filled with fresh stream water. No hatches and no spawning activities occurred in the two ponds filled with water from the ponds containing goldfish, up to September 7. At that time one of these ponds was drained and the one that was one-third full was rapidly filled with fresh stream water. Very light spawning occurred September 14, in spite of the 2 to 1 dilution of the original water. Consequently, on October 1, the water in this pond was drained to just sufficient water to hold the brood fish, and was completely refilled with fresh water. Heavy hatches were found October 15. Upon draining the following April 8, the pond was found to contain 36,164 young goldfish per acre. The three ponds originally filled with fresh stream water were found to contain 65,352, 76,042 and 86,260 young goldfish per acre.

Results of this experiment showed that the repressive factor was apparently excreted into the water by the goldfish population, that this water transferred to new ponds retained this repressive factor, and that the factor remained relatively effective in preventing reproduction even when diluted 2:1 with fresh water. It was not carbon dioxide nor pH nor oxygen content of the water because all ponds were fertilized and a good growth of plankton was present in all ponds. The fact that 2:1 dilution with fresh water reduced only slightly the repressive effect suggests that the material probably is a hormone-like excretion from the fish, effective in the control of reproduction by this species.

This information has been of immense importance in developing methods for goldfish production for bait (Prather, Fielding, Johnson, and Swingle, 1953). In production of goldfish by the egg-transfer method, from 200 to 5000 or more brood fish are placed in a brood pond and the eggs collected on mats for removal to rearing ponds. Within one to two months egg-laying usually ceased. However, by draining the brood pond and refilling with fresh water periodically it was found possible to obtain eggs as early as February and as late as the first week in November, thus extending the normal egg-laying period by 6 months.

Losses of goldfish eggs from the earliest spawns were often heavy due to sudden cold spells. Using the above information, it was found possible to prevent early reproduction by crowding the brood fish in wintering ponds several months or more prior to the spawning period. By the time the water warmed up to spawning temperature, the concentration of the repressive factor was sufficient to prevent reproduction. Light spawning occasionally did occur, however, in these wintering ponds if heavy rains freshened the water, or if a stream of fresh water was allowed to flow through the pond.

Experiments with the Common Carp. *Cyprinis carpio* Lin.

In the method of carp culture developed in Europe (Schaperclaus, 1933; Huet, 1953), reproduction is obtained by transfer of the brood carp from wintering ponds into special Dubisch spawning ponds to induce egg-laying. These small ponds are kept dry until spring, a crop of grass is grown and they are then filled with fresh water from a pond not containing carp. One or two pairs of carp are then introduced when the water temperature has reached approximately 60°F. Spawning usually results the following day. In the rearing ponds, the fingerling fish are stocked at high rates per acre and no or very little spawning occurs during the following two years of culture. Two- and three-year old fish are saved for spawners; the assumption is often made that younger fish or smaller fish cannot spawn and that this explains the lack of reproduction in the rearing ponds. Also it is often assumed that reproduction can be induced only in ponds similar to Dubisch ponds containing grasses for egg-laying.

Results of experiments conducted at the Alabama station indicated that the reproduction controls in common carp populations are the same as those found in goldfish.

A pond was stocked November 11, 1945, with 40 carp yearlings averaging 0.29 pounds each. The following spring they averaged approximately 0.5 pound by spawning time and spawning occurred successfully on March 27. This demonstrated that year-old carp as small as 0.5 pound can reproduce under proper conditions.

In another pond in this series, stocked November 11, 1945, with 500 carp per acre, also averaging 0.29 pound, carp failed to spawn. In two additional ponds stocked with 1000 carp per acre in December and fed through the following spring, spawning did not occur. This suggested that as in goldfish, heavier populations of carp built up a concentration of a repressive factor that prevented spawning.

In subsequent experiments two ponds were stocked March 3 with 1000 common carp per acre and were fed. No spawning occurred under these conditions during March, April and up to the middle of May, although their normal spawning period is late March or early April. On May 19, and May 24, ponds of equal area and free of all vegetation were filled with water from a pond that did not contain carp and the entire carp populations of the original ponds transferred to these new ponds. Spawning occurred within the next few days in both ponds. This indicated that failure to spawn was not due to a "space factor," but was due to a repressive factor excreted into the water by the carp which gradually built up to a concentration that prevented reproduction.

Reproduction has been induced repeatedly in carp by their transferral to ponds filled with fresh water for as late as two months after their regular spawning time. To date, attempts have not been made to induce spawning at later dates, although female carp full of mature eggs have been found in carp ponds as late as August 15. Also, prevention of spawning has been achieved by stocking large numbers of carp per acre in ponds well in advance of the proper spawning temperature.

The excretion by carp of a repressive factor would explain the often noted absence of spawning or the extremely light spawning in wild waters with little inflow of fresh water, and their explosive reproduction under conditions where water levels drop low in the fall, followed by great increases in water areas during floods the following spring. It would also help to explain the original abundance of carp in new impoundments constructed on rivers containing this species and their subsequent decline in abundance.

EXPERIMENTS WITH THE BIGMOUTH BUFFALO, *Megastomatobus cyprinella* Val.

The bigmouth buffalo is one of many river fishes that will not normally reproduce in ponds. Its spawning habits are similar to those of the Asiatic carps. It lives in the large rivers and reproduces at periods of floods when the rivers overflow their banks in the spring. Apparently, there is no reproduction if floods do not occur at the proper time.

Canfield (1922) early found that this fish and other buffalo fish would spawn if placed in partially filled ponds and the rest of this pond flooded at the proper spawning temperature.

Results of experiments at this Station have shown also that the bigmouth buffalo could be induced to spawn by keeping them well fed in ponds over winter and either transferring them to ponds filled with fresh water in the spring when the water temperature reached 62°F. or placing them in a partially filled pond and continuing to fill with fresh water when the 62° temperature was reached. In case spawning was delayed for several weeks due to sudden low temperatures or immaturity of the fish, it appeared necessary to partially drain the pond and refill with fresh water.

It thus appears that the bigmouth buffalo excretes a similar type of repressive factor that is effective in control of reproduction. This offers an explanation as to the necessity for floods to induce spawning in the rivers.

EXPERIMENTS WITH THE BLUEGILL (*Lepomis macrochirus* Raf.) AND LARGEMOUTH BASS (*Micropterus salmoides* Lac.)

Experiments with the bluegill indicated that probably a similar control of reproduction was present since there was a negative correlation between the rate of reproduction and the rate of stocking adult fish. However, it was ineffective in controlling bluegill reproduction to a point where overcrowding would be prevented.

Largemouth bass, however, appeared to respond to a somewhat similar method of population control. In brood ponds bass usually stopped spawning after a few schools of young bass hatched. However, if these schools were removed promptly, additional reproduction occurred by other individuals in the group. In one experiment bass were removed from a series of ponds after reproduction had ceased, and placed in ponds with fresh water. Several more schools of bass were subsequently produced. This suggests the excretion of a repressive factor into the water by the young fish, but insufficient research has been done to clarify this point.

In the bluegill-bass ponds, it was found that the excretion from bluegills apparently exerted a repressive effect upon reproduction by bass. Originally, (Swingle and Smith, 1943) it was reported that failure of bass to reproduce in overcrowded bluegill populations was due to bluegill eating the bass eggs. Although this does occur, it was later found that in overcrowded bluegill populations, bass formed eggs, but that most of these eggs were never laid. Examinations of bass in late summer indicated that the eggs were eventually resorbed.

Examination of large numbers of ponds indicated that there was negative correlation between the reproductive rate of bass and the density of the bluegill population. Extremely heavy reproduction by bass occurred only in the absence of bluegills or where bluegills were very scarce. Increasing population density of bluegills decreased the rate of bass reproduction, eventually reaching a point where bass were unable to reproduce at all.

Here was a case where the population density of one species affected reproduction of a different species. It appears again that this effect was due to excretion of a repressive material by the bluegills.

A similar effect of bluegills upon smallmouth bass (*Micropterus dolomieu* Lac.) apparently occurs as the species failed repeatedly to reproduce when stocked in combination with bluegills.

SUMMARY AND DISCUSSION

It appears that a number of species excrete into the water a repressive factor that may reduce or prevent reproduction. This material may be specific for that species or may affect other species.

The exact nature of the repressive factor is not known, but its presence was demonstrated by the experiments herein reported. By the use of this information, it was possible to prevent, or to retard or to obtain reproduction by a number of species.

This method of population control is probably widespread in nature, and it is especially important in many river fish populations. It is apparently the factor making possible the European system of carp culture, where reproduction is controlled by manipulation of the carp population.

This information offers promise of extending our knowledge of fish populations and may aid in inducing a number of important river species to spawn in ponds.

LITERATURE CITED

CANFIELD, H. L. 1922. Care and feeding of buffalo fish in ponds. *U.S. Bur. Fisheries Ec. Cir.* 96.

HUET, MARCEL. 1953. Traite de Pisiculture. LaVie Rustique. 371 pp.

PRATHER, E. E., J. R. FIELDING, M. C. JOHNSON and H. S. SWINGLE. 1953. Production of bait minnows in the Southeast. *Ala. Poly. Inst. Agr. Expt. Sta. Cir.* 112, 71 pp.

SCHAPERCLAUS, WILHELM. 1933. Textbook of pond culture. Translation by Frederick Hind; *U.S. Fish and Wildlife Service Fisheries Leaflet* 311, 261 pp.

SWINGLE, H. S. and E. V. SMITH. 1943. Factors affecting the reproduction of bluegill bream and largemouth black bass in ponds. *Ala. Poly. Inst. Agr. Expt. Sta. Cir.* 87, 8 pp.

PRODUCTION PROBLEMS OF CHANOS CULTURE IN THE PHILIPPINES

By Deogracias V. Villadolid and Herminio R. Rabanal
Bureau of Fisheries, Manila, Philippines

Fish culture in the Philippines consists principally of the raising of milkfish or "bangos," *Chanos chanos* (Forskäl). At present there are about 88,000 hectares of developed milkfish ponds involving an investment of approximately 176 million pesos (₱176,000,000.00) and the employment of some 100,000 people. The estimated yearly production of these fishponds is 31 million kilograms of fish valued at about 46 million pesos (₱46,000,000.00). Considering the fact that the Philippines produces at the present time only about half of its requirements in fish proteins and that there are 600,000 hectares of cultivable and potentially productive swamplands still undeveloped, it becomes easily understandable why more attention is being turned to the problem of Chanos culture in the Philippines. These problems are multifarious, needing urgent solution in order to place this industry on sound commercial and technical footing. This paper attempts to point out such problems which may be worthwhile bringing out for discussion among local workers and our foreign colleagues who, we are quite certain, could offer stimulating and fruitful exchange of views on this subject.

The production problems of Chanos culture in the Philippines may be presented conveniently under two categories, namely:

I. Those bearing directly on mortality or loss of the Chanos under culture.

II. Those concerning fishpond pests and nuisance which tend to increase the cost of production.

The causes of mortality may be grouped under the following:

1. Unfavorable chemical and physical factors of the environment.
2. Parasites and diseases.
3. Predators.
4. Nutritional causes.
5. Mechanical causes.
6. Mismanagement.

Fishpond pests and nuisances include:

1. Organisms destructive to fishpond dikes.
2. Organisms destructive to fishpond gates.
3. Organisms destructive to algae and other fish food materials.
4. Obnoxious pond weeds.

CAUSES OF MORTALITY OF MILKFISH

UNFAVORABLE PHYSICAL AND CHEMICAL FACTORS OF THE ENVIRONMENT

Unfavorable physical and chemical factors of the environment often occurring in commercial Chanos fishpond establishments result in the wholesale death of fish. They are in many instances hard to detect, so the unschooled fishpond caretakers are at a loss to explain such mortality, which may be attributed to one or a combination of the following factors:

1. Oxygen deficiency.
2. Pollution.
3. Turbidity.
4. "Pond kill."

Oxygen deficiency.—Many Chanos fishponds, especially the nurseries, are overstocked. Even if these are not overstocked, the water level, by necessity, is constantly kept shallow to insure the luxuriant growth of the algal food of the fish. Due to this practice, there are many instances when the oxygen content of the pond becomes so low that a fishpond operator is not able to supply the minimum oxygen requirement needed by the stock of fish in the ponds. This is a common cause of wholesale death of fingerlings in the nurseries.

High temperatures lessen the oxygen carrying capacity of the water. This, if coupled with overstocked condition, may lead to oxygen crisis and subsequent death of the fish.

Sometimes the water may go down so low in volume that the oxygen dissolved in it will not support the fish being reared. This may be caused by leaks, seepage, or continued low water.

Stagnation may also result in the depletion of oxygen. Stirring created by the incoming water, winds and waves increases oxygen in the water and replenishes the water with low oxygen with new well aerated one.

Presence of plants in the water minimizes the danger of oxygen deficiency as plants give off oxygen and use up carbon dioxide in the photosynthetic process during the light hours of the day.

Pollution.—Our common knowledge of pollution is a condition in the water wherein it is contaminated by obnoxious substances to an extent that it is detrimental to its normal aquatic life. Pollution may be caused by excessive decomposition of organic matter within the pond. This results in the rapid usage of the oxygen supply and subsequent emitting of carbon dioxide, hydrogen sulfide and other obnoxious gases.

Pollution of waters may also come from effluents of factories or industrial plants. These may carry poisonous substances actually dumped into the water or organic matter, the decomposition of which emits poisonous gases and uses up the oxygen.

Pollution from population centers is due to sewage. Sewage may be beneficial to fish cultural projects after some process of transformation and dilution; otherwise the substances dissolved in water may be in such high proportions as to cause death to aquatic life.

Turbidity.—In spite of the fact that Chanos is considered a very hardy fish with regards to its capacity to withstand very wide changes of salinity and temperature it has been found to be very susceptible and sensitive to the effect of turbidity. For this reason all efforts are being exerted in avoiding turbidity in ponds. Turbid water probably causes silting on the gills resulting in the suffocation and subsequently death of the fish.

"Pond kill".—This is a term which may be applied to a sudden fluctuation of one or more of the physico-chemical factors in the fishpond which often causes the wholesale mortality of fish. These factors may take the form of radical changes in temperature, salinity, pH, oxygen supply, turbidity or sudden appearance of obnoxious substances in the water. Under any of these conditions wholesale death of fish or a "pond kill" may result or likely to come about.

PARASITES AND DISEASES

Parasites.—Mortality due to parasites is rare if at all in Chanos. It is possible that the fish may harbor certain parasites especially when reared in fresh waters, although there is no record of this as yet.

Diseases.—A disease that has attained epidemic proportions in milkfish is the fin rot disease. This is characterized by the rotting of the fins, especially of the caudal fin, resulting in wholesale death. The cause of this disease has not been fully determined in Chanos.

PREDATORS

Predatory fishes.—The predatory fishes in the Chanos fishponds consists of a very large assemblage of varied species of fish. Some of them are predators of Chanos in the nursery ponds, others in the rearing ponds while some in both pond units.

Because of their limited size, the following have been known as predators of Chanos fry and fingerlings in the nursery stage of cultivation:

1. Family—Eleotridae, the eleotrids.
    a. *Butis* sp.
    b. *Ophiocara aporos* Bleeker.
2. Family—Gobiidae, the gobies.
    a. *Chonophorus malanocephalus* (Bleeker).
    b. *Oxyuricthys microlepis* (Bleeker).
    c. *Glossogobius giurus* Buchanan-Hamilton.
    d. *G. celebius* (Cuvier and Valenciennes).
3. Family—Periophthalmidae, the mud skipper.
    a. *Periophthalmus barbarus* (Linnaeus).
4. Family—Theraponidae, the grunts.
    a. *Therapon argenteus* (Cuvier and Valenciennes).
    b. *T. cancellatus* (Cuvier and Valenciennes).
    c. *T. jarbua* (Forskäl).
    d. *T. plumbeus* (Kner).
    e. *T. theraps* Cuvier and Valenciennes.
5. Family—Ambassidae, the glass fishes.
    a. *Ambassis batjanensis* Bleeker.
    b. *A. kopsi* Bleeker.
    c. *A. urotaenia* Bleeker.
6. Family—Anabantidae, the climbing perch.
    a. *Anabas testudineus* (Bloch).

The predatory species of fish confined in the rearing ponds are the following:

1. Family—Ariidae, the sea catfishes.
    a. *Arius leiotetocephalus* Bleeker.
    b. *A. manillensis* Cuvier and Valenciennes.
    c. *A. thalassinus* (Ruppell).
2. Family—Muraenesocidae, the pike eel.
    a. *Muraenesox cinereus* (Forskäl).
3. Family—Muraenidae, the moray.
    a. *Gymnothorax* sp.

Other species are encountered as predators of cultivated Chanos in both the nursery and rearing ponds. These include the following:

1. Family—Elopidae, the ten pounder.
    a. *Elops hawaiiensis* Regan.
2. Family—Megalopidae, the tarpon.
    a. *Megalops cyprinoides* Broussonet.

3. Family—Latidae, the sea bass.
    a. *Lates calcarifer* (Bloch).
4. Family—Epinephelidae, the groupers.
    a. *Epinephelus bleekeri* (Vaillant and Bacourt).
    b. *E. corallicola* (Cuvier and Valenciennes).
    c. *E. megachir* (Richardson).
    d. *E. merra* Bloch.
    e. *E. undulosus* (Quoy and Gaimard).
5. Family—Carangidae, the cavallas and crevalles.
    a. *Caranx deani* Jordan and Seale.
    b. *C. ignobilis* (Forskäl).
    c. *C. manillensis* Herre.
    d. *C. sexfasciatus* Quoy and Gaimard.
    e. *C. speciosus* (Forskäl).
    f. *C. stellatus* Eydoux and Souleyet.
6. Family—Lutjanidae, the snappers.
    a. *Lutjanus argentimaculatus* (Forskäl).
    b. *L. bohar* (Forskäl).
    c. *L. chrysotaenia* (Bleeker).
    d. *L. fulvus* (Bloch and Schneider).
    e. *L. johnii* (Bloch) .
    f. *L. malabaricus* (Bloch and Schneider).
    g. *L. monostigma* (Cuvier and Valenciennes).
    h. *L. spilurus* (Bennet).
    i. *L. vitta* (Quoy and Gaimard).
7. Family—Ophicephalidae, the murrel, mudfish or snakehead.
    a. *Ophicephalus striatus* Bleeker.
8. Family—Clariidae, the fresh-water catfish.
    a. *Clarias batrachus* (Linnaeus).

Amphibians.—The common frog, *Rana vittigera* Wiegmann, is often met in fishponds. It is a dangerous predator of the bangos fry in the nurseries.

Reptiles.—Predatory reptiles are represented by aquatic species of snakes and lizards. The snakes include *Disteira ornata* (Gray) or "kalabukab," and *Chersydrus granulatus* (Schneider) and *Lapemis* sp. both of which are known locally as "malabasahan."

The lizards are represented by *Varanus* sp. which are known to be active carnivores. The harm done by them may be felt in both the nurseries and rearing ponds.

Some localities in the neighborhood of fishponds harbor the swamp crocodile. This may be a menace to fishpond projects although its harm has not yet been fully ascertained.

Bird predators.—Bird predators are rampant in the nurseries. They include the kingfishers or "kasay-kasay," *Alcedo athis bengalensis* (Gmelin) and *Halcyon chloris collaris* (Scopoli); the common tern or "kalangay," *Sterna hirundo longipennis* Nordmann; the purple heron or "kandang-aho," *Ardea purpurea manillensis* Meyen; the eagle or "lawin," *Butastur indicus* (Gmelin); the bittern or "bakaw," *Butiroides striatus carcinophelus* (Horsefield) and *Ixobrychus* spp.; and the cattle egret or "tagak," *Bubulcus ibis coromandus* (Boddaert). These birds may come singly or in big flocks and cause considerable losses to the fish stock if control measures are not provided. Fishpond caretakers often acquire shotguns to kill birds. There are also varied contraptions devised for their control. Traps, scarecrows and noise scares are often installed amidst the ponds. Another innovation is to place bamboo or wooden poles at regular intervals along the fishpond dikes. To these poles, lines of cotton twines are tied so that the ponds are traversed by these lines. The birds which have the habit of diving for their prey are scared by these lines.

NUTRITIONAL CAUSES

The mortality due to nutritional causes may be attributed to the following causes, namely:

a. Starvation and other nutritional deficiencies.
b. Overfeeding.
c. Misfeeding.

Starvation.—Starvation occurs if the ponds are overstocked or when they are infertile so that they are not capable of producing food or enough of it to support the fish under cultivation. Under these circumstances the fish get starved and become very susceptible to unfavorable conditions of the environment and to diseases. Starvation can be detected when the fish have proportionately large head and a thin tapering abdomen and tail. Sometimes shiny specks occur at the bases of the fins. They become sluggish and in some instances there develops a deeper tinge of dark or black color along the dorsal region. This is sometimes believed as a condition of blindness because the fish in this state isolate themselves, losing their normal gregarious nature, and when attempts are made to catch them they are tame and are caught easily.

Overfeeding.—Overfeeding occurs if the ponds are well supplied with food, especially mature or soft filamentous green or blue green algal blooms. A few deaths have been found due to this cause. If the fish are fed by artificial feed like rice bran or "darak," care should be exercised that only such amounts as the fish can consume should be given or else continuous feeding sometimes causes bloating of the abdominal region and death.

Misfeeding.—Misfeeding is often encountered in the process of giving artificial feed to Chanos. The use of coarse rice bran instead of fine rice bran is a common cause of death in the nurseries. In other instances mortality is also brought about when the food available consists of thick blooms of filamentous blue green algae. It could not, however, be ascertained whether this is caused by wrong food or pollution from decay or over-abundance of this type of food. Misfeeding is also the result of feeding filamentous algae to the fry and fingerlings. At this stage they are not ready to feed on this type of food nor on higher aquatics, because these are tough unless they are partially decayed and their tissues softened.

MECHANICAL CAUSES

Injury and loss of scales due to rough handling.—Rough handling which results in injury to the body, fins and scales affects the vitality of the fish a great deal. After such injury, the fish lose appetite. They become sluggish and very susceptible to diseases until they finally die. All efforts should be exercised to avoid this occurrence when handling the fish.

Entanglement in thick growth of filamentous algae or pond weeds.—The fry and small fingerlings are observed to be constantly swimming actively in the ponds. When these are placed in ponds where there is a luxuriant growth of filamentous green algae and higher aquatic pond weeds, they are liable to get entangled and die. This is the reason why growths of these types of vegetation should be avoided in the nurseries. If their growth cannot be avoided, they may be gathered and piled in heaps so that they may partially decay—a state which the fingerlings can utilize for food.

Entanglement in jelly-like masses of annelid egg cases.—The presence of bulb-like mucilaginous egg cases of annelids has been observed to be of common occurrence in the nursery ponds. These egg cases have been found to belong to the Eunicidae of the polychaete annelids. What factors promote or bring about the sudden appearance or disappearance of these egg cases have not been definitely established. However, there are times when they occur in abundance. It is during these times when the fingerlings get entangled or encased in them, causing their death.

Bumping in containers, gates and other obstructions.—Chanos in all their stages of growth are very susceptible to the effects of injuries due to various causes. Some of the common symptoms indicating the effects of injuries are manifested by apparent stiffness of the body, sluggishness and refusal to feed. These could be avoided by preventing injury. It can be done by avoiding sudden stimulation of the fish in the containers or in the ponds which causes their erratic and rapid movement.

MISMANAGEMENT

Accidental drying of pond.—Occasionally due to negligence or inexperience of the caretaker, the ponds get drained causing the exposure in very little water and eventually the death of the fish. This usually happens in the nursery ponds. This shows that the caretaker should be watchful at all times of the day. Care should be exercised so that in the process of draining the pond water some allowance resulting from additional loss of water due to seepage, leaks and evaporation is taken into account.

Escape through leaks, broken gates and dikes or overflooding.—Although these are not causes of mortality yet loss of fish due to their occurrence accounts for additional cost of production. Once noticed, big leaks should be taken care of and the dikes should be reinforced as a regular measure of maintenance to prevent possible loss during big floods and other inclement weather conditions. The gate slabs and screens should be frequently examined and properly maintained at all times.

During floods all necessary measures, like the use of bamboo screens and precautions against the arrival of such inclement times, should be taken to prevent the escape of the fish.

Overstocking.—Overstocking is a common mistake of new fishpond operators. When overdone, it may result in mortality and in most instances in inferior production. In extreme cases of overstocking, especially in the nurseries, wholesale death occurs due to oxygen deficiency.

Improper container.—The problem of fish containers often leads to undue losses. Breakage sometimes occurs when earthen jars are used so that expert packing and extra care are needed to avoid breakage. Metallic containers that get heated easily or get rusty with use are also improper containers for fish. An ideal container should be one that is unbreakable and provides for aeration and cooling of the water.

Fishpond Pests and Nuisances

ORGANISMS DESTRUCTIVE TO FISHPOND DIKES

Various crustaceans with burrowing habits, especially those capable of living out of water for short intermittent periods, cause great destruction to fishpond dikes, build mounds on them which eventually lead to seepage and leaks in the dikes. Of these, the shrimp-like crab, *Thallasina anomala* (Herbst), is very common and probably most destructive. This builds up burrows on fishpond dikes. The economic swamp crab or "alimango," *Scylla serrata* (Forskäl), is another serious dike borer if allowed to grow in the ponds especially if such ponds are actually stocked with them. The burrowing nature is not only a specific characteristic but it has been observed that when the urge to spawn comes they try to seek exit from the fishpond by building burrows. Other crustaceans commonly observed to build small burrows or holes in swampy areas include a species of Potamonidae locally known as "kokomo," a species of trigger shrimps, *Alpheus* sp. and sometimes the fiddler crab or Ocypodidae. These borers are eradicated by catching and trapping them from the fishponds. To minimize the danger of leaks they cause, frequent repairs of the dikes by making deep and wide puddle trenches should be undertaken.

ORGANISMS DESTRUCTIVE TO FISHPOND GATES

Fishpond gates made of wood are vulnerable to borers of various kinds. Even the crevices of concrete gates are foci of destruction for gate borers. A member of the Peredo group, locally known as "lotus," *Martesia striata,* is one of the worst of these borers. This is common and is very destructive to wooden gates.

The rest of the gate borers are crustaceans. These include an Isoped belonging to the family Sphaeromidae, which is characterized by a hard compact body and hard jaws. It starts boring when small by making a tiny hole on the surface of the wood, increasing its burrows into the wood of the gate as it grows. The holes they make are never found to connect with each other, producing several individual holes in a damaged wooden gate. Barnacles or the Cirripedia of various types and Bryozoans also attack and foul the superficial layers of the wooden gates.

ORGANISMS DESTRUCTIVE TO ALGAE

Various types of molluscs, especially pond snails belonging to the family Cerithiidae, are very common in fishponds. They cause turbidity of the pond water and they may also feed on the algal food of the fish.

The appearance especially in enormous swarms of the megalopa stage of crabs belonging to the family Telphusidae has been found to be very destructive to algal growth. These larval forms are said to attack the algal filaments cutting them and also possibly feeding on them.

Other organisms destructive to algal growths include various types of zooplanktonic organisms such as the copepods, cladocerans and ostracods.

Herbivorous fishes and forage species that are herbivorous or omnivorous utilize algae and compete with the cultivated species.

The growth of higher aquatic plants in the ponds has been shown to be harmful to good growth of algae.

OBNOXIOUS FISHPOND WEEDS

The weed problems in fishponds consists of four types, namely:

1. Emergent rooted vegetation.
2. Submerged rooted vegetation.
3. Fringing terrestrial and semi-aquatic vegetation.
4. Surface or floating vegetation.

Emergent rooted vegetation.—This group consists of higher aquatic plants rooted in the pond substratum but their stems and leaves are erect so that they rise above the water. They cause shading of the pond bottom and because of their thick growth, they lessen the pond space for the cultivated fish. Once established these plants are very difficult to eradicate. They easily propagate by seeds and also by runners. Most of them possess tubers which, even upon the temporary death of the plant body during unfavorable environmental conditions, remain alive in the pond soil to propagate again upon the onset of favorable conditions. Upon death they are liable to pollute the pond water and because they are very tough and fibrous, they are not very useful as fish food substitute. They usually secure foothold in a pond when, after a fishpond has been cleared and allowed to be intermittently dried and exposed then flooded, the planting of the desirable pond vegetation or algae is not made.

The most common pond weeds belonging to this group are members of the family Cyperaceae. The most notable representative of Cyperaceae are *Cyperus malaccensis* Lam., *Scirpus* spp.; especially *Scirpus lacustris* Linnaeus, *Eleocharis dulcis* (Burm.) and *Fimbristylis ferruginea* Linneaus. Typhaceae is represented by *Typha* sp.

Submerged rooted vegetation.—The submerged higher aquatic plants in fishponds belong to an assemblage of several species which are collectively called "digman" locally. They compose several species which, under favorable conditions, grow very luxuriantly in the pond to reduce space for the fish, prevent the growth of the algal food and choke the water when they decay. Limited growth of this type of pond vegetation is advantageous, but excessive bloom is harmful.

The most notable representative of this group are *Ruppia maritima* Linnaeus, *Halophila* spp.; *Thalassia hemprechii* (Ehrenb.), *Najas* sp., *Anacharis* sp. and *Chara* sp. The appearance of these types of pond weeds is more pronounced during the rainy season when water salinity is low. This is true with species of Najas, Thalassia, Chara, Anacharis and of *Halophila ovata* Gaudich. However, some species are resistant to salty water and can thrive normally under this condition. These are exemplified by *Ruppia maritima* and *Halophila becarrii* Aschers.

Fringing terrestrial and semi-aquatic vegetation.—To this group belongs the coarse terrestrial vegetation growing on fishpond dikes as well as the semi-aquatic plants fringing the dikes. They provide the lairs of terrestrial and amphibian predators and contribute also in shading the pond bottom and in lessening the water space of the fishpond. The representatives of this group belong to the grass family or Gramineae. *Imperata cylindrica* (Linnaeus) or "kogon" and *Saccharum spontaneum* Linnaeus or "talahib," are coarse and undesirable vegetation of fishpond dikes. The most notable of the semi-aquatic grasses is *Paspalum vaginatum* Sw., a grass which can thrive normally even under the influence of salt and brackish water.

Surface or floating vegetation.—Dense growth of floating pond vegetation other than algae are not wanted because they shade the pond bottom, thus reducing its productivity. The plants that produce these conditions are commonly encountered in fishponds where water is of low salinity, rich in organic matter, or rather polluted. *Lemna paucicostata* Hegelm or the duck weed is known to be a fish food item but excessive growth in the ponds is harmful. Occasionally also the ponds may be invaded by a dense growth of water hyacinth, *Eichornia crassipes* (Mart.) and *Pistia stratiotes* Linnaeus. These plants, when in excess, prove to be obnoxious.

REFERENCES

1. ADAMS, W., H. R. MONTALBAN and C. MARTIN (1931). Cultivation of bangos in the Philippines. *Phil. Journ. Sci.* 47: 1, 1-38.
2. ARRIOLA, F. J., (1941). Notes on brackish water fish farming in Luzon. *Phil. Journ. Sci.* 76: 2, 105-119.
3. CARBINE, W. F., (1948). Bangos culture in the Philippines. *Progressive Fish Culturist* 10: 4, 187-197.
4. FREY, D. G., (1947). The pond fisheries of the Philippines. *Sears Found. Journ. Mar. Res.* 4: 3, 247-258.
5. HERRE, A. W. and J. MENDOZA, '(1928). Bangos culture in the Philippine Islands. *Phil. Journ. Sci.* 38: 4, 451-509.
6. RABANAL, H. R., (1949). The culture of *lab-lab*, the natural food of the milkfish fry and fingerlings under cultivation. *Dept. Agric. Nat. Res. Tech. Bull.* No. 18: 1-9.
7. ———— and H. R. MONTALBAN, (1953). The growing of algae or "lumut" in bangos fishponds. *Phil. Fisheries Handbook*, p. 142-152.

8. Rabanal, H. R., H. R. Montalban and D. K. Villaluz, (1951). The preparation and management of the bangos fishpond nursery in the Philippines. *Phil. Journ. Fisheries* 1: 1, 3-34.
9. Villadolid, D. V. and D. K. Villaluz, (1950). A preliminary study on bangos cultivation and its relation to algae culture in the Philippines. *Dept. Agric. Nat. Res. Pop. Bull.* No. 30.

Diagrammatic Representation of the Production Problems of Chanos Culture in the Philippines

- Production Problems of Chanos Culture in the Philippines
  - Causes of mortality
    - Unfavorable chemical and physical factors of the environment
      - Oxygen deficiency
      - Pollution
      - Turbidity
      - “Pond kill”
    - Parasites and diseases
      - Fin rot and minor parasites
    - Predators
      - Predatory fishes
      - Predatory amphibians
      - Predatory reptiles
      - Predatory birds
    - Nutritional causes
      - Starvation and nutritional deficiencies
      - Overfeeding
      - Misfeeding
    - Mechanical causes
      - Injury and loss of scales due to rough handling
      - Entanglement in thick growth of filamentous algae or pond weeds
      - Entanglement in jelly-like masses of annelid egg cases
      - Bumping in containers, gates and other obstructions
    - Mismanagement
      - Accidental drying of pond
      - Escape through leaks, broken gates and dikes, or overflooding
      - Overstocking
      - Improper container
  - Fishpond pests and nuisances
    - Organisms destructive to fishfond dikes
      - Burrowing crustaceans
    - Organisms destructive to fishpond gates
      - Molluscan and crustacean wood and rock borers
    - Organisms destructive to algal food of fish
      - Cerithiidae (pond snails)
      - Megalopa of Telphusidae
      - Zooplankton
      - Herbivorous fishes
      - Higher aquatic plants
    - Obnoxious pond weeds
      - Emergent rooted vegetation
      - Submerged rooted vegetation
      - Fringing terrestrial and semi-aquatic vegetation
      - Surface or floating vegetation

NURSERY POND MANAGEMENT TECHNIQUES IN PHILIPPINE CHANOS FISHPONDS

By Herminio R. Rabanal and Heraclio R. Montalban
Bureau of Fisheries, Manila, Philippines

The Philippine fishpond industry for milkfish or "bangos," *Chanos chanos* (Forskäl), is a well-established enterprise and a lucrative investment. It is known to be of very long existence and today it has attained a comparatively high degree of development. Certainly the annual production of about 30 million kilograms is a great boost to the country's fish supply. There is every prospect for its expansion gauged from the fact that the country needs more fish and there are 600 thousand hectares more of available swamplands, a large portion of which are adaptable for conversion into fishponds. The progress of this industry, however, is peculiar in the sense that it evolved not through scientific know-how but by the trial and error experience of the fishpond operators through the years. This fact is true to such an extent that local fishpond caretakers almost usually do their work as a matter of course as was handed down to them by their predecessors. In this paper we shall endeavor to explain some of the techniques developed in this fishery not only to inform but also to seek from our co-workers and foreign colleagues possible avenues for improvements on these practices. The following discussion is confined to the techniques developed in the Chanos nursery ponds in this country.

The Nursery Pond Unit in a Milkfish Pond Project

Nursery Work as One Phase of Milkfish Cultivation

The cultivation of milkfish may be divided into three distinct phases, namely: (1) the rearing of the fry and fingerlings in the nursery ponds; (2) the growing and stunting of the fingerlings in the transition ponds; and (3) the raising of fingerlings to marketable sizes in the rearing ponds (See Table I and Figure 1). The rearing ponds are the largest and deepest ponds in the system. Generally each compartment may be as small as one hectare to as large as 5, 10, 15 to 20 hectares with depth of water ranging from 0.3 to 1.5 meters. About 90 per cent of the fishpond project should be devoted to the rearing pond unit. The transition ponds are on the average about 1.0 hectare each, with the depth of water maintained at about 30 centimeters. The area allotment for this unit in a project is about 9 per cent.

About one per cent of the area of the fishpond project should be alloted to the nursery ponds. These are the shallowest ponds in the system. They are made thoroughly clean and well-tended. Each pond ranges from 500 to 5,000 square meters, with the depth of water during operation maintained generally at not over 30 centimeters. Here the seed fish consisting of bangos fry are stocked. The fry are reared until they attain the fingerling stage which ranges from 4.0 to 10.0 centimeters in length. Because bangos fry are available only once during the year, the fingerlings are kept stunted at these sizes to provide a reservoir of stock for the rearing ponds after each cropping. One to four crops of marketable sizes may, therefore, be raised from the rearing ponds each year.

Selection of Nursery Site

Careful consideration should be taken in selecting the nursery site in a fishpond project as success depends a great deal on this unit. It should be located where the soil is fertile and where the topography is more or less level. It is generally built in the most elevated portion of the area. In relation to the source of water supply, it should be very accessible. It is best to have the nursery ponds built in a site which is clear and devoid of thick growth of forest trees in order to avoid the great difficulty of clearing and cleaning the area thoroughly.

Layout and Construction of Nursery Ponds (Refer to Figure 2)

The nursery unit in a milkfish pond establishment consists of the nursery ponds proper, catching ponds, water supply canals and the necessary water supply gates, pipes and screens needed for effective water control. Usually the nursery ponds are of equal sizes and are arranged regularly in series alongside a water supply canal. There should be provided a catching pond for each nursery pond or one catching pond for every two adjacent nursery ponds.

The water supply which should be readily available to the ponds may be taken in through a main water control gate or pipe which may be made of wood or of concrete. Water is often conveyed from the main gate to the nursery ponds through a water supply canal. A cylindrical or quadrangular pipe connects the water supply canal with the catching pond. From the catching pond the water is conveyed through a wooden gate or pipe to each pond. All the pipes and gates used in water conveyance and control should be well screened with either metal, bamboo or cloth screen during the rearing period of the milkfish fry and fingerlings.

NURSERY POND MANAGEMENT TECHNIQUES

Cultivation and Leveling of Pond Bottom

The techniques necessary to bring about success in the management of the nursery ponds are actually employed right from the beginning or when these ponds are prepared before they are stocked with fry. First of all, the pond bottom is loosened by actual cultivation or turning over of the soil. This makes available the essential nutrients of the soil which may be in the subsurface layers of the substratum. Besides, the loose soil is a more favorable medium for the growth of the suitable food of the fry and fingerlings.

Cultivation is followed by a careful leveling of the loose soil in such a manner that the bottom slopes vary gradually from the sides of the ponds down to the gate. Sometimes there may be established a sort of depression or a canal that runs diagonally from the gate to the farthest side or corner of the nursery ponds. This will be a safety canal where the fish can secure refuge during very warm days or when the ponds get accidentally drained. The above procedure of leveling provide these safeguards as well as the necessary means in effecting drainage in order to facilitate the total capture of the fish whenever desired or to clean out the ponds of extraneous species.

Water Management to Effect Growth of the Desirable Fish Food Organisms

After the nurseries have been properly leveled they are drained completely to clean off all other aquatic organisms. This is followed by a period of drying the bottom by exposing it to the sun in order to kill other resistant species in the pond. The pond bottom is continuously exposed until it cracks. This takes about two weeks to two months to accomplish. It has been observed that ponds which have undergone this process are not only totally cleaned but when water is allowed into them thereafter a more luxuriant growth of fish food organisms is produced than when partially dried only.

The nurseries undergo a process of "washing" which consists of letting in water during the high tide and draining it out again during the low tide intermittently for a few times, the purpose being to wash out any crystallized salts left on the pond bottom during the drying process. By this method it is also possible to kill some of the resistant burrowing organisms which may still be lying dormant in the pond bottom. This has been observed to be especially true with a species of predatory eel, *Synbranchus bengalensis*, which upon the first entrance of new tidal water, comes up to the surface of the mud only to be killed when the pond bottom is drained again.

The above procedure is followed next by letting in and impounding water in the nurseries, and regulating its depth to effect maximum growth of the desirable fish food organisms. At the beginning, water just enough to cover the pond bottom (3 to 5 centimeters) should be introduced. Under this state, within a period of 3 days to a week, the growth of micro-benthic biota locally known as *lab-lab* develops on the pond floor. The depth of the pond water is then gradually increased as the *lab-lab* grows thicker up to about 10 to 30 centimeters. For best results the water should not be allowed to go beyond this depth, otherwise filamentous green algae which is not needed at this stage of cultivation, may develop. It seems that the exposure to heat and intense light of the pond bottom with shallow water stimulates the growth of the micro-benthic organisms. It is possible that the development of filamentous green algae is a normal occurrence in the ecological succession of generation brought about in a comparatively deeper water of the pond, but the rapid and extreme fluctuation of conditions due to shallow water maintained in the nurseries keeps the simpler micro-benthic fauna and flora to continue to flourish.

Water freshening is the process of changing the stagnant, very saline and stale water in the ponds with clear and well oxygenated water of lower salinity brought in by the incoming tide. This kind of water favors better growth of fish food organisms so that freshening and effective circulation should be undertaken in the fishpond nurseries. Excessive stirring of the pond bottom should, however, be avoided in the process and flood water or turbid freshets should not be used in freshening the nursery ponds.

Screening the Nurseries During Water Management

After the thorough draining and drying of the pond and after water is introduced, great precaution is exercised by having the gates and pipes properly screened and closed with the necessary materials. This is necessary to prevent the entrance of the eggs, larvae or adults of organisms which may be potential predators of milkfish fry and fingerlings. After stocking, these fine screens will likewise prevent the possible exit of the tiny fish that have been released in the nursery ponds.

There are several methods used to screen the nurseries effectively. In case of gates and quadrangular pipes, bamboo splits or wire netting mounted on wooden frame may be used. These screens may still be quite coarse and it may become necessary to have them reinforced with abaca fiber cloth, locally called "sinamay," before the fry are planted. The sinamay cloth remains in use until the growing fish have attained a size big enough so they cannot escape through the bamboo or wire screen. In the case of cylindrical water pipes a sort of screen basket made of bamboo splits is used. This is devised to provide facility for water passage as well as prevent the exit of the cultivated species or entrance of extraneous ones. This screen is likewise reinforced with abaca fiber cloth before stocking as well as during the early cultivation period.

Stocking Rate and Stocking Procedure

Milkfish fry for cultivation in the fishponds are tiny, elongate and almost transparent. They are caught in the fishing grounds situated in certain definite areas along sandy coastal shores or in tidal streams during a certain season of the year, generally from as early as March to as late as July. Upon arrival of the fry in the fishponds, the caretaker makes an estimate of the total approximate number and carefully sorts out the other species mixed with them before actual stocking is undertaken.

The stocking rate depends on the amount of suitable fish food available and the area of the fishpond nursery. Nursery ponds with good growth of *lab-lab* or those where the entire pond bottom is covered by luxuriant growth of this fish food can accommodate normally from 300,000 to 500,000 fry per hectare (30 to 50 fry per square meter) to prevent large scale mortality and insure a normal rate of growth of the cultivated fish during a period of one to two months. Understocked nurseries or those stocked with intensity of less than 30 fry per square meter would be an expensive procedure because comparatively less fish would be reared for a unit area, whereas, if they were overstocked or with stocking intensity much beyond 50 fry per square meter, wholesale mortality or early stunting of the fish may be experienced, resulting in the production of inferior quality of stock.

Experienced fishpond caretakers have found out that the best time for stocking the fry would be in the early mornings or late afternoons on a fair day. These colder periods of the day would avoid undue mortality during this very critical period in the life of the fish under cultivation. Under certain exigencies the fry may be released anytime of the day but after new water is introduced into the ponds.

The milkfish fry are contained in the earthenware containers of 15 to 20 liters capacity. In releasing these fry, the containers with the fish are brought to the nurseries usually near the gate area which is supposed to be the deepest portion of the nursery pond proper. The caretaker takes a container and very carefully lowers it to the water in this deep area. He then tilts this container to allow small amounts of the pond water to flow into the jar. If the temperature or salinity difference between the water in the jar and the pond water is great, the period of pre-mixing should be prolonged. When a sufficient amount of the pond water has filled the jar, this is tilted further and skillfully lifted gradually to let out all the fry into the ponds without disturbing the water so much.

Stunting Milkfish Fingerlings

As has been previously mentioned, the milkfish seeds for stocking the fishponds are the tiny elongate fry and these fry can be obtained only in certain coastal shores and tidal streams during a definite period of the year. It is quite fortunate that under the present extent of the industry the quantity of fry obtained during this definite period from the known fry grounds is quite sufficient. However, if the growth of the young milkfish under cultivation could not be supervised to advantage for fish cultural purposes, a seasonal crisis of the supply of stock would occur each year. The happy solution in this regard is the ability to stunt milkfish fingerlings as long as desirable to supply a steady stock even during the transition between fry seasons without in anyway endangering the capacity of the stock to grow to normal marketable quality and size when placed under suitable conditions. This is the reason for the necessity of stunting the fingerlings with the nurseries acting as reservoir of stock for the rearing ponds for a year round operation.

The milkfish fry caught from the fishing grounds are 10 to 15 millimeters long. Under favorable conditions in the nursery ponds, they attain the fingerling stage within one to two months. At this stage, they vary in sizes ranging from 40 to 100 millimeters in length. This is the range of fish sizes generally kept in the nurseries and stunted for a prolonged period. At this stage, the fingerlings need a minimum amount of food. They can be confined in a more limited space and are easy to handle for purposes of counting, sorting and transplanting. It has been observed that these sizes could be maintained from the normal period of two months of rearing to as long as two years in properly managed nursery ponds.

Stunting is generally looked upon as an improper procedure for sound fishpond management because it may produce unfavorable effects on the normal rate of growth of the fish. However, in milkfish culture this practice is being utilized to advantage and with very favorable results. In fact fishpond caretakers managing rearing ponds exclusive of nurseries would demand the stunted fingerlings when buying their stock because they have found them to be more hardy and more adapted to the new type of food conditions in the rearing ponds. Stunted fingerlings have also been found to be more capable of avoiding their enemies than the non-stunted ones.

It is also common knowledge among experienced fishpond caretakers that the rate of growth of stunted fingerlings is as good or even better than the non-stunted ones when such fingerlings are stocked in the spacious rearing ponds where their natural food is abundant.

Managing Overstocked Ponds

In nurseries managed by well-trained caretakers overstocking is a rule. This is because of their desire to raise a large number of fish in a minimum space and to manage the growth of such a stock in the manner deemed fit.

Stock dispersal.—"Stock dispersal" is a process in which a small unit of the nursery is utilized for the rearing of a comparatively large number of fry, and the growing fish are dispersed to the adjacent nursery units as soon as necessity occurs. For instance nursery ponds could receive as high as 200 fry per square meter at the beginning. This is actually stocking a tremendously large number, which may lead to disastrous results if not properly managed. In a period usually not extending two weeks, a nursery pond will show the exhaustion of the fish food and apparent crowding of the stock so that an adjacent nursery pond of probably equal area is opened where the growing fish could disperse. This newly opened unit has its *lab-lab* intact and its water well-conditioned, thus allowing the fish to attain normal if not rapid growth. The dispersal shall have reduced the stocking rate per unit area and as growth continues it is possible that within a two-week to one month period the growing stock has become crowded again. Another nursery pond unit is again opened to further disperse the fish and this process is repeated as soon as there are indications of crowding and whenever there are still nursery pond units available. In this way, fingerlings of uniform size and good quality can be produced.

Fractional transplantation.—Another method for managing overstocked ponds may be termed "fractional transplantation." Fractional transplantation is a process in which a selected portion of a crowded stock of fish is transplanted in order that the stocking rate may be reduced to normal limits. This is very appropriate in overstocked ponds because of the diversity of the sizes of fingerlings in such ponds coupled with the ease in confining separately the larger batch in a stock. Whenever it is noticed that the stocking rate of a nursery becomes intolerable due to overstocking, water is allowed into the ponds and the fish readily go against the current to be confined in the catching pond. The first group of fish entering the catch pond consists of the larger sizes in a stock. This batch is isolated and caught for transplantation purposes. It is generally observed that while these larger sizes attain the fingerling stage, the rest of the stock may be too small for transplanting purposes. The batch of smaller sizes is, therefore, left in the nursery for further rearing, thus removing the imminent danger of an overstocked state. The selected larger sizes may, therefore, be transplanted into the transition pond for further growth or into the rearing pond until they attain marketable sizes.

Sustenance feeding.—The supply of the natural food in the ponds under optimumly stocked ponds and overstocked conditions last within a period of about two months at most. In nurseries with poor soil and under improper management, the fish food may be deficient even shortly after stocking. Under these circumstances, particularly in overstocked ponds where the food is consumed within a short period, the remedy is by "sustenance feeding." Sustenance feeding is a process by which the stock of fingerlings in the nurseries is maintained in healthy and stunted state by giving them just sufficient artificial feed. The amount of food will vary with the stocking rate and the sizes of the fingerlings and this may be determined after a few trials. The artificial feed found suitable is fine rice bran. As a result of recent experimentation, corn bran has been discovered as a good if not better substitute. The optimum quantity of rice or corn bran for an area of nursery pond with certain amount of stock of growing fish is that amount which when fed to the fingerlings is totally consumed but in sufficient amount to sustain the health of the fish. The sign of overfeeding is indicated by the presence of unconsumed feed, and mortality due to bloated intestinal tract while underfeeding is indicated by the presence of sickly and thin fish. Feeding is usually done twice a day, once in the morning and once in the afternoon, and the result is to be keenly observed in order to determine the amount necessary for sustenance feeding. Once this is determined the process could be continued almost indefinitely without much material change in the size and condition of the fish. The nursery can thus serve as a reservoir of bangos fingerlings from which the supply for transplantation can be obtained whenever and wherever needed.

SUMMARY

1. Milkfish or bangos cultivation is an extensive and well-established industry in the Philippines. A specialized and well-developed

phase of this industry is the management of the milkfish nursery ponds.

2. Only about one per cent of the area of a bangos fishpond project is alloted to the nursery unit. This unit should be located in a site where the soil is clayey and fertile, which is slightly elevated and devoid of thick forest growths, and which has ready access to the water supply.

3. The various pond compartments and their auxiliaries, including the gates and pipes, should be well laid out to provide effective water control and circulation.

4. The nursery ponds are meticulously prepared before the stocking of the fry. First the pond bottom is stirred or cultivated to provide a loose consistency and also to make available the essential nutrients which may be in the sub-surface layers of the substratum. It is carefully leveled so that it will slope very gradually from the extreme sides toward the nursery gate which should be the deepest portion of the pond proper.

5. The nurseries are drained and the pond bottoms are exposed to sunlight for days until they dry up completely and crack. This will result in the complete eradication of fish predators and competitors of the cultivated species.

6. The level of the pond water in the nurseries can be so regulated to effect the luxuriant growth of the desirable fish food organisms. This is accomplished by allowing just enough water to cover the pond bottom at the start and by increasing the depth as soon as a good growth of micro-benthic fauna and flora or *lab-lab* had developed. The water level is, however, maintained not to exceed 30 centimeters so that higher types of vegetation unsuitable for fish food at this stage may not grow.

7. The gates and pipes for water control in the nursery ponds should be carefully screened, especially during the period before the fry are planted up to the early part of the culture period. Screens of bamboo splits and wire netting mounted on wooden frames are used. These are further reinforced with the abaca fiber cloth in order to avoid the entrance of foreign species and prevent the escape of the fish under cultivation.

8. The normal stocking rate for milkfish nursery ponds is 30 to 50 fry per square meter. Understocked nurseries would prove expensive because of the waste of space. On the other hand overstocked nursery ponds, if not carefully managed, may result in the wholesale mortality of the fish.

9. Techniques developed in milkfish nursery ponds have led to the well-established practice of stunting fingerlings. The fishpond operator takes advantage of this practice because the supply of fry comes from

the fishing grounds only once a year, and in so doing, it is possible for him to obtain readily stunted fingerlings anytime when needed for release in the rearing ponds. According to this practice, marketable-sized fish can be raised from two to four times a year from the same pond.

10. Overstocking the nurseries is a general practice in the well-developed fishpond areas in the Philippines. However, a well trained fishpond caretaker has learned to counteract the unfavorable consequences which may be brought about by overstocking. By some improved techniques, a comparatively large amount of stock could be derived per unit of space.

One method of managing overstocked nursery ponds is by stock dispersal. This is a process in which a large stock is placed in a very small unit of a nursery pond and later dispersed in the adjacent nursery units until the normal stocking rate is attained.

11. A second method of managing overstocked ponds is by fractional transplantation. This is accomplished by isolating and transplanting the batch of larger sizes of an overcrowded stock until the normal stocking rate is reached.

12. Artificial feeding of bangos fingerlings is resorted to after the natural food in the pond has been consumed. The discovery of fine rice bran and lately of corn bran for this purpose, is indeed an achievement of the milkfish pond caretakers. Overstocked nursery ponds are properly managed by controlled feeding, a process which we have termed as sustenance feeding. This is a method by which just enough feed is used to sustain the fish in good health but in stunted condition. Artificial feeding is deemed necessary in order to maintain the stock for replenishing the rearing ponds.

REFERENCES

1. ADAMS, W., H. R. MONTALBAN and C. MARTIN (1931). Cultivation of bangos in the Philippines. *Phil. Journ. Sci.* 47: 1-38.
2. CARBINE, W. F. (1948). Bangos culture in the Philippines. *Progressive Fish Culturist* 10: 194-197.
3. PREY, D. G. (1947). The pond fisheries of the Philippines. *Sears Found. Journ. Mar. Res.* 4: 3, 247-258.
4. HERRE, A. W. and J. MENDOZA (1928). Bangos culture in the Philippine Islands. *Phil. Journ. Sci.* 38: 451-509.
5. MANE, A. M., D. K. VILLALUZ and H. R. RABANAL. (1952). Cultivation of fish in brackish and estuarine waters in the Philippines. *Phil. Fisheries*—handbook prepared by technical staff, Bur. Fisheries. Manila: 100-110.
6. RABANAL, H. R. (1949). The culture of lab-lab, the natural food of the milkfish fry and fingerlings under cultivation. *Dept. Agric. Nat. Res. Tech. Bull.* No. 18: 9 pp.

7. RABANAL, H. R. (1949). Pond culture of warm water fishes (With special reference to bangos or milkfish cultivation under Philippine conditions). U. N. Scientific Conference on Conservation and Utilization of Resources. *Wildlife* 4(e), 7.

8. ————, R. S. ESGUERRA and M. M. NEPOMUCENO (1952). Studies on the rate of growth of milkfish or "bangos" *Chanos chanos* (Forskäl) under cultivation. 1. Rate of growth of the fry and fingerlings in fishpond nurseries. *Proc. 4th Indo-Pacific Fisheries Conf. Tech.* 15.

9. ————, H. R. MONTALBAN and D. K. VILLALUZ (1951). The preparation and management of the bangos fishpond nursery in the Philippines. *Phil. Journ. Fisheries* 1:1, 3-34.

TABLE I

SUMMARY OF THE SCHEME OF CULTIVATION IN A COMPLETE CHANOS FISHPOND PROJECT BASED ON A 10-HECTARE AREA

	Nursery Pond Unit	*Transition Pond Unit*	*Rearing Pond Unit*	*Production*
Area	1000 sq. m. (1% of area)	9000 sq. m. (9% of area)	90000 sq. m. (90% of area)	90% of stock or equal to 4500 kg./yr. (based on 500 kg./ha. jr.)
Number and Size of compartments	May be 1 but 2 or more ponds of not less than 500 sq. m. each are preferred	May be 1 although 2 or more ponds preferred of variable size but comparatively bigger than nurseries	May be 1 although 2 or more ponds preferred, varying from 1 to 10 hectares in area	
Stocking Rate	30,000 to 50,000 fry (30 to 50 fry per sq. m.)	Variable, on the average 1 fingerling per sq. m.	On the average 1 fish per 10 sq. m. or range of 0.5 to 2.0 fish per 10 sq. m.	
Time of Stocking	April, May or June each year	Any time expedient	Anytime expedient as ponds are ready	
Frequency of Stocking	Once a year	As many as necessary	Once to 4 times in a year as frequently as pond conditions permit	
Duration of Rearing	At least 2 months to an indefinite period	At least 1 month to an indefinite period	From 3 months to 12 months per crop	
Rate of Survival	50% (range of 10 to 90%)	90% on the average	90% on the average	
30000 to 50000 fry stocked to	15000 to 25000 fingerlings stocked to	13500 to 22500 post fingerlings stocked to		
	50% mortality	10% mortality	10% mortality	

TABLE II

TYPE CALENDAR FOR CHANOS NURSERY POND PROJECTS

FEBRUARY *	1. Complete clearing of the nurseries to be stocked. 2. Preparation of nurseries—patching and cleaning dikes; clearing, cultivation and leveling, and draining of ponds. 3. Harvest of last year's stock of marketable fish and preparation of transition-rearing ponds.
MARCH	1. Complete the preparation of nurseries—draining and drying of pond bottom. 2. Letting in of water to grow fish food organisms—*lab-lab.* 3. First stocking of the transition-rearing ponds, from leftover fingerlings. 4. Disposal of stunted fingerlings (old stock).
APRIL	1. First stocking of the nurseries (partial). 2. Continue the disposal of stunted fingerlings. 3. Rear fish in stocked nurseries and maintain lab-lab growth in unstocked ones. 4. Rear fish in transition-rearing ponds.
MAY	1. Continue stocking of the nurseries. 2. Rear fish in stocked nurseries and maintain lab-lab growth in unstocked ones. 3. Rear fish in stocked transition-rearing ponds. 4. Complete disposal of stunted fingerlings from nurseries if possible.
JUNE	1. Complete stocking of the nurseries. 2. Second harvest of marketable fish and preparation of transition-rearing ponds. 3. Manage stock of fish in the nurseries—dispersal of stock, artificial feeding and water management. 4. Possible disposal of new-stock fingerlings.
JULY	1. Continue management of stock of fish in the nurseries. 2. Possible disposal of new-stock fingerlings. 3. Second stocking of the transition-rearing ponds.

* February starts the seasonal activities in nursery pond projects.

AUGUST	1. Continue management of stock of fish in the nurseries. 2. Possible disposal of medium-aged fingerlings. 3. Rearing of fish stocked in transition-rearing ponds.
SEPTEMBER	1. Continue management of stock of fish in the nurseries. 2. Possible disposal of medium-aged fingerlings. 3. Rearing of fish stocked in transition-rearing ponds.
OCTOBER	1. Continue management of stock of fish in the nurseries. 2. Possible disposal of medium-aged fingerlings. 3. Third harvest of fish and preparation of the transition-rearing ponds.
NOVEMBER	1. Continue management of stock of fish in the nurseries. 2. Possible disposal of stunted fingerlings. 3. Third stocking of the transition-rearing ponds.
DECEMBER	1. Continue management of stock of fish in the nurseries. 2. Possible disposal of stunted fingerlings. 3. Rearing of fish stocked in transition-rearing ponds.
JANUARY	1. Continue management of stock of fish in the nurseries. 2. Sale and disposal of stunted fingerlings so nurseries can be cleaned. 3. Rearing of fish stocked in transition-rearing ponds.

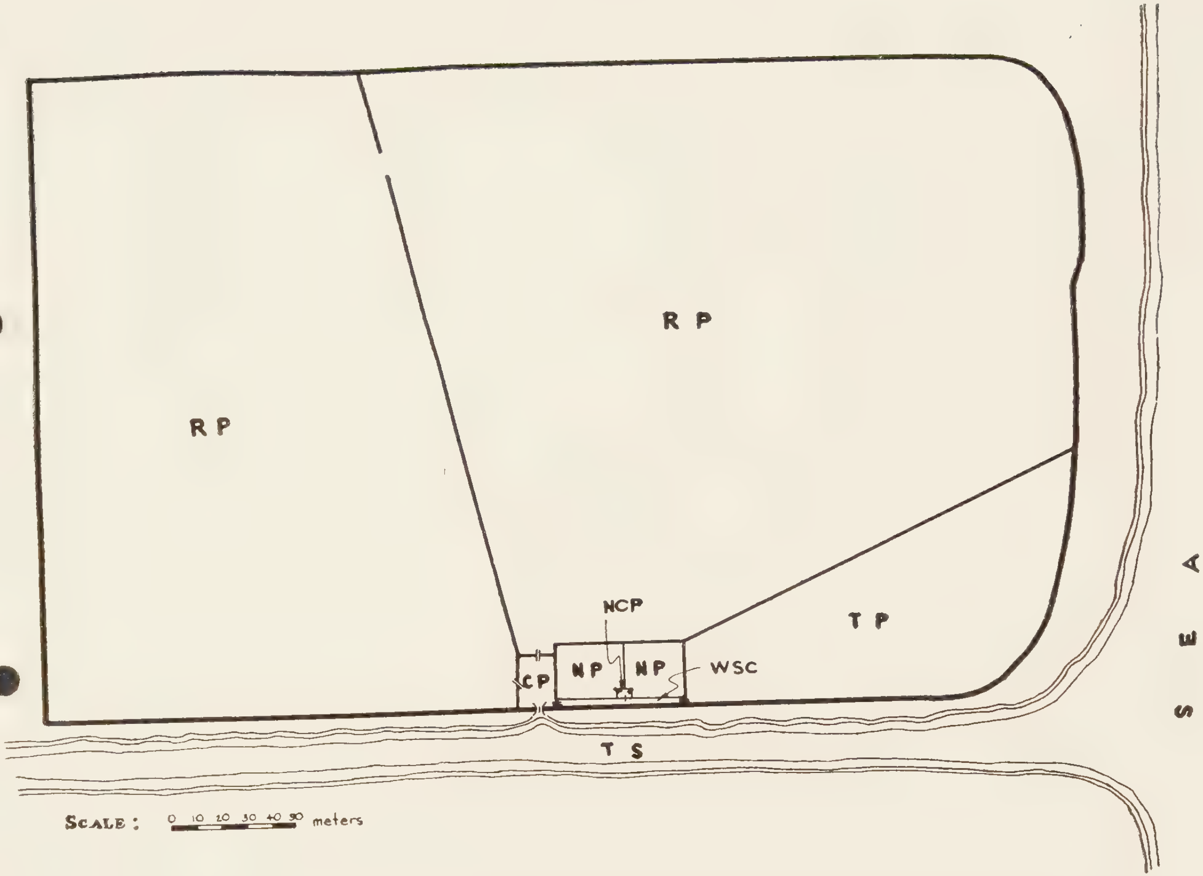

R P
R P
T P
NCP
NP
NP
CP
WSC
T S
S E A
SCALE : 0 10 20 30 40 50 meters

FIG. 1.—MODEL LAYOUT FOR A 10-HECTARE COMPLETE CHANOS FISHPOND PROJECT. CP, catching pond; NP, nursery pond; NCP, nursery catching pond; RP, rearing pond; TP, transition pond; TS, tidal stream; WSC, water supply canal; ⟩|⟨, main gate; (double-opening); —¦—, secondary gate; —|—, pipe.

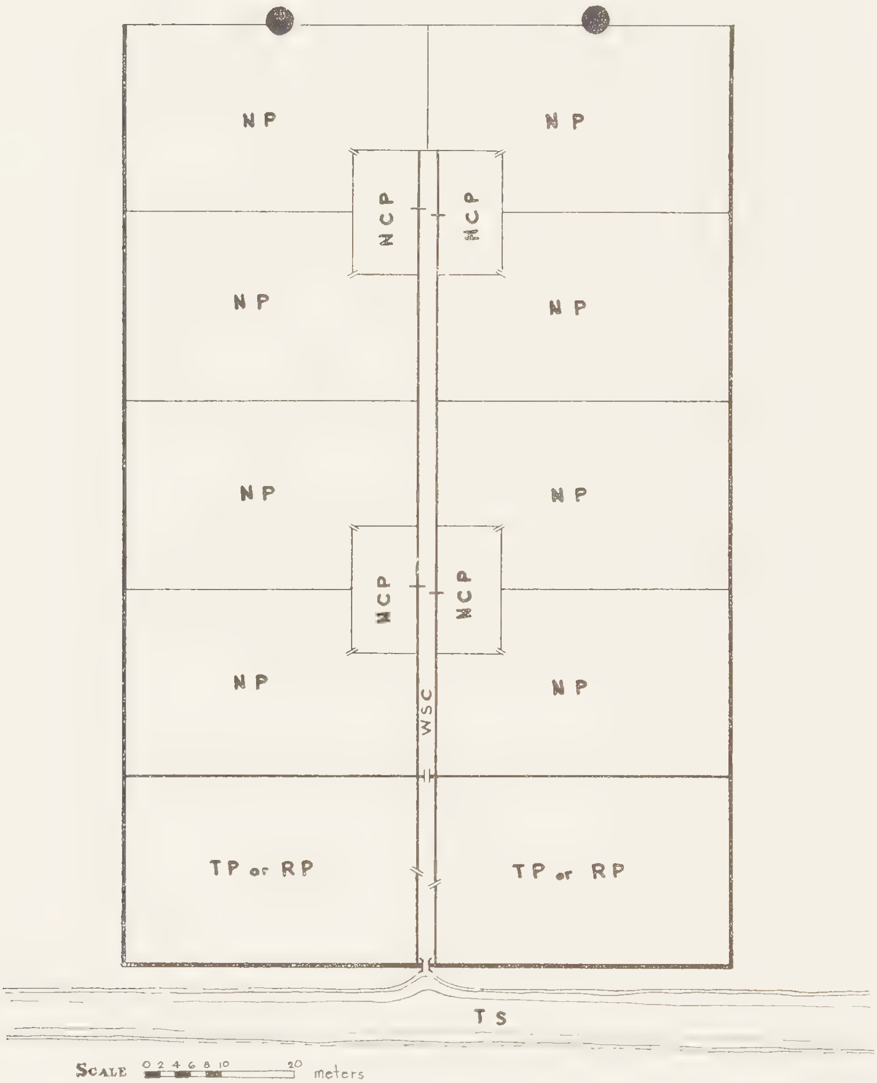

N P
N P
N C P
N C P
N P
N P
N P
N P
N C P
N C P
N P
N P
WSC
TP or RP
TP or RP
T S
SCALE 0 2 4 6 8 10 20 meters

FIG. 2.—MODEL LAYOUT FOR A 1-HECTARE CHANOS NURSERY POND PROJECT.

—)(—, main gate (single-opening); —||— or —\\—, secondary gate;

—╤ nursery gate.

November 24, 1953

SYMPOSIUM ON ECOLOGY OF CORAL ATOLLS

Convener: Dr. Robert W. Hiatt, Hawaii Marine Laboratory, University of Hawaii, Honolulu, Hawaii.

Secretary: Mr. Artemio M. Sarenas, Bureau of Fisheries, Manila.

PROCEEDINGS

Session started at 8:30 A.M. Dr. Hiatt gave a few remarks on the importance of knowing the value of corals in the building of atolls. The attached program was followed and Dr. Hiatt further announced that the speakers have very limited time and questions will be entertained at the end of the symposium. There were no questions asked to any of the speakers, except the few remarks given to some of the papers read by about two or three members of the audience. These remarks were neither clearly recorded nor important enough for their inclusion in this report.

Symposium ended at 2:30 P.M. with the convener, Dr. Hiatt, expressing his appreciation and gratitude for the success which he accredited to the members who cooperated faithfully and patiently attended the meetings.

The papers were presented as follows:

1. Introductory Remarks—Harold J. Coolidge, U. S. National Research Council, 2101 Constitution Avenue, Washington 25, D.C., U.S.A.
2. The Geology of Atolls. Joshua I. Tracey, Jr., U. S. Geological Survey, Box 218 Agana, Guam.
3. Observations sur les Falaises et les Phosphates de Makatea (Ile des Tuamotu)—le Probleme de la Consolidation, des Sèdiments. Gilbert Ranson, Museum National d'Histoire Naturelle, Paris, France.
4. The Hydrology of Atolls. Ted Arnow, Ground Water Branch, Water Resources Division, U. S. Geological Survey, Agana, Guam.
5. An Enumeration of the Hypothetical Roles of Algae in Coral Atolls. Maxwell S. Doty, University of Hawaii, Honolulu, Hawaii.

6. Factors Influencing the Distribution of Corals on the Reefs of Arno Atoll, Marshall Islands. Robert W. Hiatt, Hawaii Marine Laboratory, University of Hawaii, Honolulu, Hawaii.
7. Scaridés et Milieu Corallien: Notes Biogéographiques. Théodore Monod, Muséum National d' Histoire Naturelle, 57 rue Cuvier, Paris 5e, France.
8. Observations sur les Facteurs Biologiques de la Dissolution du Calcaire D'Origine Récifale dans les Tuamotu. Gilbert Ranson, Muséum National d'Histoire Naturelle de Paris, France.
9. Observations sur les Iles Basses des Tuamotu, Océanie Francaise. Gilbert Ranson.
10. Nature and Origin of Atolls—A progress report. Preston E. Cloud, Jr., U. S. Geological Survey, Washington 25, D.C., U.S.A.
11. Soils, Vegetation and Agriculture on Coral Atolls. F. R. Fosberg, Pacific Vegetation Project, National Research Council, Washington 25, D.C., U.S.A.
12. Relation of Humans to the Atoll Environment. Alexander Spoehr, Bernice P. Bishop Museum, Honolulu 17, Hawaii.

ADDITIONAL PAPERS SUBMITTED

13. Crustacés Decapodes Paguridae D'Oceanie Francaise. Jacques Forest.
14. Observations sur L'Epoque de la Reproduction de *Pinctada margaritifera* (L.) et de quelques autres Organismes Marins dans les Tuamotu. La Cause du Nanisme de *P. margaritifera* (L.) dans le Lagon de Takapoto. Gilbert Ranson.

INTRODUCTION TO SPECIAL SYMPOSIUM ON ECOLOGY OF CORAL ATOLLS

By Harold J. Coolidge
National Research Council, 2101 Constitution Avenue
Washington 25, D.C., U.S.A.

The Pacific Science Board of the National Academy of Sciences—National Research Council is engaged in a program of research on the ecology of coral atolls in the Pacific. These studies are principally supported by the Geography Branch of the U. S. Office of Naval Research.

The Board's Atoll Program is associated in its origin with Project E.6 of the Research Council of the South Pacific Commission. While the Commission project is concerned directly with the improvement of the economy and welfare of atoll peoples, the Board's research is fundamental to a basic scientific understanding of atoll problems, and involves an ecological approach to the study of environmental factors affecting life on coral atolls which may furnish us with a scientific means of determining the carrying capacity of a given atoll.

The type of investigation which will lead to complete understanding of the geography of an atoll requires as basic information a complete knowledge of the physical situation and the local organisms therein, including their characteristics, requirements, and behavior. In addition, there must be a knowledge of processes that are taking place in the atoll, and the effect of these processes on each other and on the various organisms.

The Board's program is, therefore, concerned with the relatively simple environment of oceanic atolls, as well as the terrestrial and marine life that is found there. The term "simple" refers to the fact that there are no problems of altitude, the atolls are tropical and oceanic in climate, their structure conforms to a recognized pattern, and the terrestrial plants and animals are limited to a few species, which, however, does not hold true for the marine life. Added to these factors are the differences in atolls depending upon variations in rainfall, variability in size and location, as well as the history and culture of the native inhabitants.

The initial program has been divided into a series of five field projects, and the compilation of an annotated bibliography of over 2000 titles of literature dealing with plants, animals, and terrestrial aspects of the atoll environment.

The field projects during the past four years have been carried out on inhabited atolls by research teams made up of a geologist, a marine biologist, an ichthyologist, an algologist, a land ecologist who was generally a botanist, and a cultural anthropologist, in addition to graduate student assistants. A total of thirty-five individual scientists have participated in the field work, with sixteen working at Arno in the Marshalls, six at Onotoa in the Southern Gilberts, six at Raroia in the Tuamotus, and seven at Ifaluk in the Western Carolines. Their research has been particularly facilitated by the cooperation that was extended by the High Commissioner of the Western Pacific and the Administration of the Gilbert and Ellice Islands Colony, by the Governor of French Oceania, by the High Commissioner of the Trust Territory of the Pacific Islands, and by the U. S. Department of the Navy and the U. S. Coast Guard.

As this program progresses comprehensive zoological and botanical collections are brought back to the U. S. National Museum and to the Bernice P. Bishop Museum. Many taxonomists in American and foreign museums are at present engaged in assisting in the identification of these collections, and in preparing handbooks to facilitate the working up of such little known groups as the Indo-West Pacific Decapoda. Information on the progress of the atoll work is being regularly circulated through the Atoll Research Bulletin, of which twenty-three numbers have been issued to date. The field teams have been aided by the Handbook for Atoll Research, which is revised in the light of increasing knowledge, and which helps to assure that all aspects of the work are given consideration. In addition to technical reports, a general natural history report is being prepared for each atoll that has been studied.

This meeting offers an opportunity to participate in a symposium on the Ecology of Coral Atolls with a panel of speakers that includes at least one member of each of the four atoll field teams, as well as two members of the Board's advisory committee on this atoll program. We hope that as a result of this meeting our colleagues from other Pacific countries will not only take an increasing interest in atoll problems, but will undertake projects coordinated with ours to increase our knowledge of the geography of atolls.

THE GEOLOGY OF ATOLLS *

By Joshua I. Tracey, Jr.
U. S. Geological Survey
Agana, Guam

Atolls are built by communities of organisms in a uniform tropical oceanic environment. They are relatively unaffected by continental land masses, but are responsive in their growth to prevailing currents, tides, and waves of the ocean. They are especially affected by storms.

The reefs show definite zones—a seaward wave-resisting margin, generally made up dominantly of crustose calcareous algae; an outer reef flat on which corals flourish abundantly; and an inner broad reef flat dominantly of Foraminifera and green or brown algae. Lagoons are bounded by a belt of coarse to fine debris near the reefs; large areas in the central basin are dominantly *Halimeda* and its debris, with scattered patches and knolls of coral that are proportionately more abundant in small and shallow lagoons than in deep large ones. Islands are formed of sand, gravel, and boulders derived from the reef. They rest in most places on lithified conglomerate or slightly raised reef rock, in a few places on unconsolidated sediments of the reef. The sediments of the islands are formed almost completely of calcium carbonate. Other minerals and elements are present only to the extent that they are originally concentrated in calcite and aragonite by organisms, or are later added by animals.

The uniformity of an oceanic environment is greatly influenced by the presence of an atoll. Water that crosses the reef is modified by photosynthesis of plants and by respiration of plants and animals. Circulation of lagoon water, initiated and maintained by tides and by wind-driven currents, distributes organic material produced by the reefs, thereby increasing the productivity of the lagoon.

Circulation of water over reefs is impeded by the presence of islands. Erosion and solution to the windward of islands and deposition to the leeward results in a lagoonwide migration of some islands.

Some islands appear to be growing, but others show a net loss in area, especially because of severe storms, that may be significant during the time that man has inhabited atolls.

---

* Publication authorized by the Director, U. S. Geological Survey.

OBSERVATIONS SUR LES FALAISES ET LES PHOSPHATES DE MAKATEA (ILE DES TUAMOTU)—LE PROBLEME DE LA CONSOLIDATION, DES SEDIMENTS.

Par Gilbert Ranson
Museúm National d'Histoire Naturelle de Paris, France

Resume

I. The Cliffs of Makatea

Makatea is an ancient elevated atoll, the lagoon of which is dry. Dana and Couthouy have already noted that Makatea and Niau were two ancient elevated atolls, with summits rising respectively to 100 m. and 5 m. above sea level: The cliffs of Makatea plunge abruptly into the sea, sometimes without any surrounding coastal shelves. The caves in the cliffs, although they appear at a same level, have not been produced by sea erosion. Similar holes are found at different levels in the interior of the island where they must have been caused by dissolution of sediments through rain. Between the caves no traces of any action by the sea are apparent. Hence, the long-standing theory entertained by many geologists that the caves were carved by the sea must probably be abandoned. The fact that they are at the same level can be explained by assuming that, in the course of the atoll's formation, the process of subsidence was interrupted by pauses or elevations during which sand or stones were deposited at various points at that particular level.

The elevation must have been rather abrupt; there are many signs which confirm this view, first set forth by Gardiner for the elevated reef of Fidji. All the coastal margins underwent various degrees of sinking, the sinking portions settling into the sea at different levels and some of them remaining partly in the air above the water. The latter were later abraded by the waves to various extents.

II. The Phosphates of Makatea

When speaking of phosphates one usually thinks of guano. But there are other sources of phosphates.

Mollusk shells and pieces of coral are not composed solely of minerals but of calcified organic matter. The latter forms the organic substrate (4 to 10%) which is the fundamental element of the object and of all its structural details. In it, calcium carbonate appears in the shape of micro-crystals perhaps as large as a protein macromolecule.

One cannot consider the coral islands of Tuamotu as mountains of calcium carbonate in a strict sense, for they are, in reality, gigantic masses of calcified organic material. The acidity of the environment, which has various causes, plays an important role in the future fate

of the organo-calcareous rocks. The existence of this acidity is best proved by the fact that all molluscan shells have been totally dissolved. As a result of this acidity, the organo-calcareous mass of the rocks is split into two components. The limetone segregates, constituting conic masses which tend to form clusters of calcite macro-crystals. The organic matter, on the other hand, becomes the source of phosphate which accumulates in the spaces betweeen the cones of limestone. Thus we have here a non-guano source of organic phosphate.

III. The Problem of the Consolidation of Sediments

The splitting of the material of organo-calcareous rocks into two constituents is sometimes a rapid process, as in the case of the Makatea phosphates. But it is not always so fast, it can be much slower, in fact, it can be extremely slow. The process may be started by various factors, such as humus, bacteria, the vicinity of volcanic rocks, which all seem to act by acidifying the medium. They work on the sediments both from within and without, acting on the inner structure as well as on the surface of separate granules of limestone; as it coalesces, the calcium carbonate granules fuse together at the points of contact, thus paving the way for macro-crystallization, which is the final and stable form of limestone. Between the micro-crystals of organic limestone (consisting of calcite or aragonite) and the macro-crystals of pure calcite, there are all sort of intermediate stages. It is thus that the pieces of corals, mollusk shells, etc. of varying size are finally welded together into one mass. At Hikueru one can actually see how this welding and consolidation of organo-calcareous gravel takes place in the presence of acid humus.

I. Les Falaises

Je n'ai pas à décrire ici l'Ile de Makatea. Elle l'a été maintes fois. On sait que Darwin considérait que les Tuamotu se trouvent dans une zone d'affaissement parce que formés d'atolls qu'il croyait "actuels." [1] Mais Darwin n'avait pas visité les Tuamotu. Les premiers observateurs Dana et Couthouy qui y sont allés se sont bien rendu compte immédiatement que Makatea et Niau étaient, de toute évidence, deux îles ayant subi un soulèvement récent, assez prononcé pour Makatea puisque son sommet est à plus de 80 mètres du niveau de la mer.

Lorsqu'on fait le tour de l'île en bateau on est frappé surtout par les falaises verticales de sa côte. On est tellement habitué à penser à l' "abrasion marine" lorsqu'on se trouve en présence de falaises que l'esprit cherche ici encore les traces de cette abrasion. On se dit tout naturellement qu'il n'est pas possible que tous les débris de l'oeuvre de destruction des vagues soient disparus. On cherche des "témoins" qui existent partout sur les autres côtes. Et l'on est fort étonné de cons-

---

[1] Lorsque j'emploi l'expression "atolls actuels," je veux dire, bien entendu, que la surface seulement est formée de coraux vivants.

tater que par endroits la falaise plonge directement dans les profondeurs, sans plateau côtier la bordant.

Un fait saute aux yeux, dès l'abord, qui vient appuyer l'idée d'abrasion. Des excavations nombreuses se présentent dans cette falaise. Elles sont, horizontalement, au même niveau. Il en existe deux rangées dit Dana, 5 ou 6 disent d'autres auteurs. Cela dépend, en fait, de l'endroit où l'on se trouve. Mais l'alignement horizontal parfait de ces excavations plus ou moins éloignées les unes des autres, n'en est pas moins impressionnant et il fixe la pensée. Tous les auteurs s'y sont laissé prendre. Il est admis que ces lignes d'excavations représentent d'anciens niveaux successifs de la mer. Ces grottes sont considérées comme représentant le travail des vagues pendant plusieurs pauses lors de la surrection de l'Ile. Il est tout de même extraordinaire que la mer, travaillant à divers niveaux successifs, ait réussi, chaque fois, c'est-à-dire 5 ou 6 fois à aboutir au même plan vertical! Il est plus logique d'admettre dans ce cas que la falaise fut coupée dès le début, à la base. Puis l'Ile aurait été submergée; enfin dans une troisième phase, s'élevant progressivement, avec de brèves pauses, les excavations auraient été creusées successivement le long de la paroi verticale. Dans ce cas nous devrions voir, entre les excavations, des traces de l'action de la mer, une ligne d'usure, tout au moins, même légère. Mais je les ai cherchées en vain.

Je n'ai trouvé qu'une trace de l'action de la mer sur la falaise, en certains endroits. Elle est à 1m, 80 du niveau du plateau côtier, la mer actuelle battant seulement le pied de la falaise. Il s'agit de tout autre chose, qui n'a aucun rapport avec les grottes en question. J'en parlerai ailleurs. Je la signale néanmoins pour bien attirer l'attention sur le fait que les vagues lorsqu'elles travaillent à un même niveau de la falaise, pendant un certain temps, laissent une trace qui est bien nette.

Cependant, on ne peut encore se défaire de l'idée que les excavations sont l'oeuvre de la mer qui en aurait extrait les sédiments consolidés qui s'y trouvaient enfermés. J'en ai visité deux de la ligne inférieure. On y trouve d'admirables stalactites. Leurs parois inférieures sont tapissées de sédiments consolidés fortement cristallisés; mais il n'y a ni galets ni autre reste, à mon avis, du passage de la mer à ce niveau.

Ainsi il m'apparut que ces excavations n'étaient pas l'oeuvre de la mer. En montant la falaise à Mumu par un chemin entre les murs verticaux de calcaire corallien, on rencontre d'autres excavations, (en particulier une véritable grotte souvent signalée) du même ordre ou même plus profondes. A l'intérieur de l'Ile on trouve également de nombreuses cavernes et crevasses. *Elles sont toutes le fait de la disso-*

lution par les eaux de pluie des sédiments consolidés qui y étaient contenus. Certaines renferment de l'eau douce en permanence.

Mais si nous comprenons maintenant l'origine des cavernes de la falaise côtière, il reste à expliquer pourquoi elles sont disposées en lignes horizontales, car c'est surtout ce dernier fait qui attire plus particulièrement l'attention. Si elles étaient distribuées irrégulièrement elles ne donneraient pas cette illusion à laquelle on se laisse prendre si facilement.

Que représentent ces lignes horizontales de cavernes? Sans aucun doute des niveaux de pause et peut être même de soulèvement du récif, avec formation d'amas de sable ou de galets sinon sur des plages, du moins dans des anfractuosités du récif, peut être même à la surface du plateau côtier comme on en voit dans certaines îles. La subsidence se poursuivant, le sédiment consolidé fut enveloppé par les coraux continuant à croître. Après le dernier soulèvement, les eaux de ruissellement ont fait leur oeuvre, d'ailleurs pas partout: c'est ainsi qu'à Niau j'ai vu des poches encore pleines de sable, en partie phosphaté, alors que d'autres sont vides ou pleines d'eau douce que la population pompe pour son usage.

Ce seul indice sur lequel on pouvait s'appuyer pour étayer l'hypothèse de l'abrasion marine disparaît. Le plateau côtier quand il existe ne révèle absolument rien de ce qui s'est passé.

La seconde fois que j'ai fait le tour de l'île, avant de la visiter à nouveau, j'ai été frappé par le fait qu'en certains endroits la falaise n'est past totalement à découvert, si je puis dire, mais qu'elle a devant elle et attenant encore à elle, ce que j'ai appelé des "avan-scènes" et qui ne sont que des portions plus ou moins importantes du bord de l'île, qui se sont effondrées à des niveaux d'ailleurs très différents les uns des autres, selon, vraisemblablement que la pente sous-marine était plus ou moins abrupte. Les unes ont disparu dans les grandes profondeurs; là le plateau côtier est inexistant. Les autres n'ont dépassé que de très peu le niveau de l'eau. Elles ont été abrasées et il en est résulté un plateau côtier plus ou moins large. D'autres enfin sont plus ou moins élevées au-dessus du niveau de l'eau et leur abrasion est en cours comme on peut facilement s'en rendre compte.

Cette notion d'effondrement de portions marginales de la côte étant entrevue, il apparaît alors clairement que les régions du Port et de Mumu sont des zones d'effondrement plus importantes que les autres.

Gardiner, en 1898 (²), a émis l'idée suivante, pour des récifs soulevés des Fidji: "considering the known sections of atoll-reefs, the precipitous cliffs to the sea can only be accounted for by the splitting off a great

---

[2] Gardiner. *Proceed. Cambridge Phil. Soc.*, vol. IX, 1898, p. 417.

masses of the rock, owing to undermining, and their subsequent solution or the formation on them of the fringing reef." Et plus loin l'auteur dit "one is driven from this to the conclusion that elevation must have taken place for each island in one act."

Davis (3) connaissait cette hypothèse de Gardiner. Il la cite. Mais il n'en continue pas moins à essayer de l'adapter à l'hypothèse des cavernes creusées par la mer.

Je pense que le soulèvement de Makatea aussi bien que de Niau n'a pas été progressif. Il a dû être assez brutal. La structure en pans de mur verticaux de certaines portions côtières donnent une idée de la puissance de la poussée.

Je ne pense pas cependant que les effondrements côtiers soient le fait d'une action de la mer à la base. Ils sont plutôt la résultante de porte-à-faux de portions, plus ou moins crevassées par la surrection violente.

II. Les Phosphates

Comme le disent Lipman et Shelley en 1924 (4), dans leur étude sur le sol de l'île Rose, chaque fois que l'on parle de phosphates, on se croit obligé de penser aux oiseaux et au guano. C'est ainsi que dans sa belle synthèse sur la biogéochimie de l'excrétion des Vertébrés, G. E. Hutchinson (5) ne manque pas de parler des atolls phosphatés du groupe des Tuamotu et autres îles soulevées, à phosphates, comme Ocean et Nauru, en particulier. Certes dans des régions voisines, nous avons des îles à guano comme les Malden et autres. Dans les Tuamotu il y a quelques îles à oiseaux (des Sternes) (6), aux Marquises aussi. Mais le guano ne se conserve que dans les zones de perturbations climatiques (climat désertique ou sub-désertique).

Il est probable que le phosphate dans certains cas, a une autre origine.

Les analyses du sol de l'île Rose, comparées avec celles d'échantillons de Lithothamion (Algue calcaire dont le sol de cette île est essentiellement composé) montrent qu'après lessivage du calcaire, le sol s'est enrichi en P_2O_5.

Makatea, est bien à mon avis, un ancien lagon dont le fond est soulevé au-dessus du niveau de la mer. C'est très nettement l'impression que j'ai eue après avoir escaladé la falaise au village de Mumu, par le sentier souvent cité, en descendant vers la zone intérieure où l'on extrait le posphate. J'arrivais de Hikueru et de Takume où, en plon-

---

[3] The Coral Reef problem. *American geogr. soc., spec. publ.*, n^0 9, 1928.

[4] Papers from the Department of Marine Biology of the Carnegie Institution of Washington, vol. XIX, 1924.

[5] *Bull. American Museum Nat. Hist. New York*, vol. 96, 1950.

[6] Christian Jouanin, Note surla *Sterna fuscata* L. en Polynésie francaise. *L'Oiseau et R.F.O.*, vol. XXIII, 2^0 tr., 1953, p. 149.

geant en maints endroits, j'étais parvenu à me faire une idée assez nette de l'aspect des fonds de leurs lagons: couverture générale de sable sur laquelle se dressent des collines et pitons sous-marins, s'élevant à tous les niveaux. La dépression de Makatea m'apparut comme un lagon fossile, dont le sable, les pitons et les collines avaient subi de grandes transformations et où l'on ne retrouvait plus de ces dernières que des restes ou "témoins," parfois importants, sous forme de blocs plus ou moins larges, plus ou moins hauts, les "feos" comme on les désigne localement. Certes, l'érosion y a fait un travail considérable, mais pas au point de penser, comme Agassiz, que l'île était autrefois un immense plateau. Elle aurait pu, tout au plus, être un lagon totalement comblé. L'érosion aurait agi plus rapidement sur les sédiments consolidés du centre que sur la couronne extérieure de corail compact. Un lagon comblé, est un lagon où le sable s'est amoncelé progressivement, enveloppant et enfouissant totalement les collines et pitons coralliens qui s'élèvent du fond, ainsi que les pierres et blocs divers rejetés par la mer du plateau côtier.

C'est l'image que nous aurions à peu de chose près si les lagons de Niau et d'Anaa par exemple étaient vidés de la faible épaisseur d'eau qui leur reste. Il existe d'anciens petits lagons totalement comblés et asséchés.

A partir de cet instant que s'est-il passé? Comment se sont transformés ces sédiments accumulés dans cette immense cuvette? Pour le comprendre il me faut faire une petite diversion. Tout d'abord, il faut que l'esprit cesse de voir dans ces amas gigantesques de productions animales que sont les îles coralliennes, de simples tas de pierre ou de sable.

A diverses occasions, j'ai insisté sur le fait qu'une coquille d'huître, un morceau de corail etc. . . ne sont pas de simples masses minérales, de simples morceaux de carbonate de chaux. *En fait, c'est de la matière organique, calcifiée.* Si le calcaire y est plus important en poids, c'est le *substratum organique* secrété par le manteau de l'animal qui joue le rôle prépondérant dans la forme de la coquille du Mollusque. C'est lui qui impose au calcaire son mode cristallin et sa dispersion. Si l'on dissout lentement, avec un acide faible, le calcaire, le substratum organique subsiste avec la forme de la coquille. J'ai employé une image pour fairé ressortir l'importance de ce fait: j'ai dit que la matière organique était "l'âme" de la coquille. Tous les plus petits détails (individuels, spécifiques, génériques, etc.) de la structure aussi bien de la coquille que du squelette du corail et des autres organismes calciques ne sont pas le fait du calcaire, mais bien du substratum organique qui a une architecture moléculaire particulière propre à l'espèce considérée.

Toutes les coquilles de Mollusques, de Foraminifères, les squelettes des Coraux, ceux des Echinodermes, des Poissons, des Algues calcaires etc. . . autrement dit toutes les productions calcaires animales ou végétales sont constituées de la même manière. Elles contiennent de 4 à 10% de matière organique. Or dans les îles coralliennes des Tuamotu, il n'y a que de telles productions. Le sable, lui-même, n'est formé que de coquilles de Foraminifères et de petits morceaux de coquilles ou de squelettes d'autres organismes. C'est donc uniquement un sable organo-calcaire. C'est pourquoi il ne convient pas, comme on le sait, à la fabrication du mortier.

Si l'on est pénétré de cette idée qu'une île corallienne (des Tuamotu par exemple) est une montagne de matière organique calcifiée et non pas seulement de carbonate de calcium, alors bien des faits s'expliquent clairement.

A la matière organique de cette origine, s'ajoute celle des Poissons, qui ont dû pulluler à un moment de l'histoire du lagon et peut être trouverait-on encore d'autres sources de matière organique.

Lorsque le lagon s'est soulevé, nous savons ce qui s'est passé en examinant se qui a lieu à Niau, où seule a été mise à nu la bordure de l'ancien lagon. Le lagon (riche en Poissons) de cette dernière île, contient, à l'heure actuelle, de l'eau saumâtre de densité 1012; et la bordure émergée de l'ancien lagon est, au moment des pluies, un véritable marécage. A mesure que le lagon de Makatea s'est soulevé davantage, son eau s'est infiltrée par les différentes poches sédimentaires souterraines, et, bientôt, s'est asséché. Les pluies en ont fait un marécage, où les bactéries ont commencé leur activité. Le sol, de ce fait, est devenu acide. Tout le calcaire a été dissout. On peut voir partout des moulages internes (phosphatisés d'ailleurs) des Mollusques qui vivaient alors. Leurs coquilles ont totalement disparu. Même si l'on ne reconnaissait pas l'intervention des bactéries dans le processus que nous décrivons, on est absolument obligé d'admettre l'acidité importante du sol, à un moment donné de l'histoire du lagon.

Ainsi s'est opérée la séparation entre la matière organique et le calcaire. Ce dernier s'est rassemblé en amas plus ou moins cristallins qui ont un aspect très spécial de cônes, laissant entre eux, des vides, des poches, où s'est rassemblée la matière organique qui a donné le phosphate.

III. Consolidation des Sediments

Nous avons assisté là à une séparation assez rapide, du calcaire et de la matière organique. Mais il n'en est pas toujours ainsi. Le phénomène est en général très lent. Je voudrais l'examiner rapidement d'un peu plus près. Nous sommes tout naturellement amenés à envisager le problème de la consolidation des sédiments qui apparaît ainsi sous un jour tout à fait nouveau, à la lumière de cette notion de "matière organique calcifiée."

Dans la coquille, comme dans toute autre production animale calcifiée, le calcaire est dans le substratum organique à l'état de microcristaux si petits que seuls les rayons X peuvent les déceler et encore indirectement. Ils sont probablement à l'échelle des grosses molécules protéiques. Leur liaison avec la matière organique est extrêmement forte car elle résiste à l'épreuve du temps. Des calcaires crétacés (anciennes Algues calcaires) m'ont donné à la décalcification une forte proportion de matière organique.

Sous certaines actions extérieures qui restent à déterminer et qui peuvent être variées sans doute, la combinaison organo-calcaire se détruit soit par départ de la matiere organique, soit par dissolution du calcaire qui peut recristalliser soit par remaniement interne. De toute manière même dans ce dernier cas, la matière organique abandonne la combinaison et dès lors le calcaire a tendance à reprendre son indépendance, si je puis dire, et à se diriger vers sa forme stable, qui est le gros cristal de calcite. Les microcristaux de calcaire (calcite ou aragonite) ont tendance à se fusionner pour former des macrocristaux rhomboédrique de calcite. Mais entre les 2 stades ci-dessus, il y a beaucoup d'intermédiaires et, chaque fois, nous avons une structure particulière de la combinaison organo-calcaire. Il suffit de simples traces de matière organique, et même dans certains cas d'autres substances pour modifier le mode cristallin de la calcite. L'évolution progressive de ce remaniement interne de la combinaison est presque toute la diagenèse.

Ce phénomène n'est pas particulier à ce minéral. Les travaux de Gaubert ([7]) ont montré qu'il est général. Par ailleurs les recherches que je poursuis depuis quelques années m'ont amené à montrer (je l'ai fait connaître récemment ([8]), que le mode orthorhombique (ou aragonitique) du calcaire chez les êtres vivants est bien le fait de la nature du substratum organique. Des expériences d'analyse et de synthèse même sont en cours à ce sujet.

Lorsque l'on casse un morceau de calcaire corallien fossile ou subfossile, on peut constater sur les parois des petites excavations internes, l'existence de gros cristaux de calcite. A ce niveau le calcaire est parvenu à s'isoler totalement du substrat et à s'individualiser. C'est une géode en miniature.

---

[7] P. Gaubert. *Bull. Soc. fr. Min.*, t. XXV, p. 258, 1902.
P. Gaubert. *Bull. Soc. fr. Min.*, t. XXXVIII, p. 149, 1915.

[8] G. Ranson. *C.R.A.S.*, t. 234, p. 1485-1487, 1952.

Pour passer du mode aragonitique où il se trouve dans le corail, au mode calcitique, il doit se débarrasser progressivement mais totalement de son substratum. Lorsque deux morceaux de corail ou de coquilles de mollusques ou des grains de sable corallien ou autre, etc. . . actuels, se trouvent et demeurent en contact (sédiments actuels) ces processus de remaniement dont je viens de parler, se produisent non seulement au sein mais aussi au contact de deux morceaux ou grains, de telle sorte que les combinaisons intermédiaires y prennent naissance et que la consolidation s'opère. On s'explique alors fort bien l'existence entre les grains de la "roche de plage" d'aiguilles d'aragonite comme vient de le montrer Ginsburg (9). Mais ces aiguilles ne sont pas des éléments surajoutés, ce n'est pas un ciment venu de l'extérieur. C'est la fusion de produits du remaniement interne et externe de deux pièces en contact.

L'idée de Cloud (dont j'ai parlé ailleurs) que la consolidation des sables pourrait être l'effet de l'apport par une Algue, d'oxalate de calcium par exemple, cimentant les éléments, est trop simple. La résistance du sédiment consolidé n'aurait rien de commun avec celle qu'on lui connaît.

A quelle cause extérieure rattacher le remaniement de la combinaison organo-calcaire des sédiments côtiers dans les régions tropicales provoquant leur consolidation si rapide en certains cas.

Je n'ai pas l'intention de traiter ici toute la question. Je ne rappellerai pas toutes les hypothèses qui ont été émises à ce sujet. Mais il semble bien que toutes se ramènent à une acidification plus ou moins prononcée du milieu, qu'il s'agisse de l'action de l'humus, des Bactéries, ou de la présence dans le voisinage de roches éruptives. (mètamorphisme de contact).

Je voudrais toutefois signaler rapidement une observation que j'ai faite à Hikueru en 1952. Il existe du côté lagon sur la côte Est de la couronne d'îlots, des mares d'eaux plus ou moins stagnantes. La mer y parvient de temps à autre. Il y pleut à la saison humide. Deux espèces de Poissons y vivaient. Du côté de la plage, la bordure de cette mare est en pente très douce. Mais du côté de l'îlot la dénivellation est d'un mètre environ. Des cocotiers s'élèvent tout près. Le roc n'est pas apparent; le sol n'est constitué que par du sable. Maist il contient une quantité appréciable d'humus. Le clapotis de l'eau a sapé la base de ce qu'on peut appeler la dune et en certains endroits, il existe une véritable petite falaise, parce que le sable commense à s'y consolider. La couleur noire de cette petite falaise est due à la présence d'une quantité d'humus appréciable. Il faut frapper assez violemment avec le pied ou

---

[9] *Journal of Sedimentary Petrology*, vol. 23, 1953.

avec une pierre pour en détacher un morceau. Ce n'est pas le cas un peu plus loin où il y a peu ou pas d'humus.

Ainsi nous assistons là d'une manière très spectaculaire à la consolidation du sable corallien en présence d'humus. On sait la réaction acide des sols d'humus, ce qui nous ramène aux considérations exposées précédemment.

A Makatea la séparation a été brutale et massive. Le calcaire s'est rassemblé comme je l'ai dit, en masses ayant la forme de cônes (que l'on retrouve dans d'autres îles à phosphate), l'examen d'échantillons pris dans ces cônes, indique que la macrocristallisation est parfois réalisée, mais dans l'ensemble il y persiste encore, un faible substratum.

THE HYDROLOGY OF ATOLLS *

By Ted Arnow
U. S. Geological Survey
Agana, Guam

The only source of fresh water on any island in an atoll is the rain that falls directly on the island. The rain water seeps into the ground and, because it is lighter than salt water by the ratio of about 40/41, it floats on the surface of the salt water. The fresh-water surface assumes the rough shape of a dome, the edges of which coincide with the edges of the island. The fresh water displaces a volume of salt water equal to its own weight and depresses the fresh water-salt water interface below sea level under the island. Under ideal conditions in a homogeneous island, because of the 40/41 weight relationship of fresh to salt water, the interface lies about 40 times as far below sea level as the fresh-water surface stands above sea level. Actually, the shape of the fresh-water body varies, depending upon local geologic conditions, and the 40-to-1 depth ratio is modified by the existence of a transition zone of variable thickness in which there is a mixture of fresh and salt water. This double-convex fresh-water body floating on sea water is known as the Ghyben-Herzberg lens. It is the only source of potable ground water on any atoll.

Fresh water is miscible with salt water, and the Ghyben-Herzberg lens will not form or will be destroyed unless there is a favorable balance of the four factors that affect the lens. The first controlling factor is precipitation. In order to build up a fresh-water lens the annual precipitation must be great enough to provide adequate recharge to the lens in spite of the small infiltration area offered by the islands in atolls and in spite of high evapotranspiration losses which may dispose of a large part of the total precipitation. Furthermore, the precipitation cannot be concentrated wholly in one short season, lest the fresh-water lens degenerate during the ensuing dry season. In the northern Marshalls it was found that no atoll supported a fresh-water lens where the annual rainfall averaged less than 45 inches. On Onotoa Atoll in the Gilbert Islands Cloud[1] found a fresh ground-water lens where the annual rainfall averaged about 40 inches. The annual rainfall fluctuates greatly at Onotoa, however, and during drought years the lens reportedly degenerates in all except the widest parts of the islands, with the resultant death of breadfruit and even salt-tolerant coconut palms.

---

* Publication authorized by the Director, U.S. Geological Survey.

[1] Cloud, P. E., Preliminary report on geology and marine environments of Onotoa Atoll, Gilbert Islands; *Atoll Research Bull.* No. 12, December 15, 1952.

The second factor affecting the ground-water lens is the permeability of the rocks and unconsolidated deposits that form the island. The permeability must be sufficiently high to allow infiltration of a substantial portion of fresh water (from rain) but not so high as to allow free mixing of the fresh and salt water. Atoll islands consist mainly of sand and gravel overlying a consolidated reef platform, and both the sand and gravel and the reef platform have a degree of permeability that is conducive to the formation of a Ghyben-Herzberg lens. The lens may be poorly developed, however, on the windward sides of some islands which are formed by boulders and other very permeable deposits.

The third factor affecting the ground-water lens is the magnitude of tidal and seasonal fluctuations of the water table. These fluctuations serve to increase the rate of diffusion between the fresh and salt water and thereby to enlarge the zone of transition and reduce the zone of fresh water. If the fluctuations are large enough the transition zone will grow until it encompasses the entire lens, thereby, in effect, destroying it as a source of potable water.

The magnitude of the tidal fluctuations in the ground-water lens at any given point is directly proportional to the permeability of the rocks between that point and the shoreline and is inversely proportional to the distance to the shoreline. On very small islands the ocean tides pass through the land practically undamped, resulting in such free mixing of fresh and salt water that a fresh-water lens does not form.

The writer has no data concerning the magnitude of seasonal or annual fluctuations of the fresh-water lens on atolls. Wentworth [2] has suggested, however, that the range of fluctuation must be less than half of the mean water-table head if the lens is to be preserved.

The fourth factor affecting the ground-water lens is the size and shape of the island. The island must be wide enough to damp the effects of tidal fluctuations sufficiently so that the fresh-water lens is not prevented from forming. It must also be large enough to catch sufficient rainfall to build up a lens of such magnitude as to survive through the dry season of the year. Cloud [3] reported that at Onotoa 1,000 feet was the probable minimum width required to maintain a fresh-water lens continuously through extended drought periods. At Ifalik Atoll in the Caroline Islands, where the average annual rainfall is more than 100 inches, a fresh-water lens was found on an island only 700 feet wide and only 0.04 square mile in area.

---

[2] Wentworth, C. K., Factors in the behavior of ground water in a Ghyben-Herzberg system; Pacific Sci., v. 1, no. 3, p. 176, July 1947.

[3] *Op. cit.*, p. 14.

It should be emphasized that the ground-water lens is not a static body nor does it represent a closed system. It is in a state of dynamic equilibrium in which the controlling factors all function simultaneously and continuously either to destroy or to build up the lens. When the balance of the controlling factors is unfavorable the lens will be nonexistent or at best will contain potable water only during the rainy season. When conditions are favorable the lens will contain potable water throughout the year.

At best the lens is thin. In the northern Marshalls the average position of the water table is only about a foot above mean sea level where it is highest, and of course it is lower at places closer to the shore. At Ifalik, early in the rainy season, the average height of the water table above mean sea level at its highest point was 1.4 feet; at the place of measurement the island is 1,050 feet wide. No data are available regarding the thickness of the fresh-water lens below sea level, but undoubtedly the depth of potable water does not exceed 40 feet for every foot of head above mean sea level, and it may be substantially less in most islands.

The quality of the water at the top of the lens varies, but where the lens is well developed the water at the top is definitely potable. In the northern Marshalls during the dry season the ground water in parts of the larger islands of six atolls contained less than 250 parts per million of chloride and in three additional atolls contained less than 500 parts per million of chloride. Water having a chloride content greater than 250 to 500 parts per million has a noticeable taste, depending on the sensitivity of the person drinking it, but water containing up to 1,000 parts per million of chloride can be drunk safely for indefinite periods of time. Water in the open sea generally contains 18,000 to 20,000 parts per million of chloride. In places at Onotoa, Cloud found the ground water to contain less than 300 parts per million of chloride. At Ifalik, during the rainy season, ground water on three of the four islands in the atoll contained less than 125 parts per million of chloride.

The use of ground water by man varies in different localities. In the Marshalls ground water is not considered particularly desirable for drinking. The fluid in young coconuts and rain water are much preferred. Rain water, when available, is actually preferred for all purposes, but when the supply is low, ground water is used for cooking, bathing, and washing clothes. During times of emergency, however, when neither rain water nor young coconuts are available, ground water is the sole source of drinking water. In Ifalik, on the other hand, practically no rain water is caught and ground water is used for drinking, cooking, and washing. At least two basic food plants, taro and breadfruit, have a low salinity tolerance and will not grow successfully where a permanent fresh-water lens does not exist. Successful taro and breadfruit were noticeably absent in atolls north of 11 degrees of latitude in the Marshall Islands, where the annual rainfall averages less than 50 inches.

Even the coconut palm, which has a much higher salinity tolerance than either taro or breadfruit, has certain minimum hydrologic requirements. At Ifalik, where the rainfall is more than 100 inches, palms bearing large nuts were observed growing on a small island that had maximum dimensions of 150 by 75 feet and an area of only 0.0004 square mile. Although the ground water was saline, the palms evidently were able to obtain sufficient fresh water directly from the zone of soil moisture because of the heavy rainfall. The annual rainfall at Taongi and Bikar in the Marshalls averages less than 45 inches. At Taongi, where the chloride content of the ground water was found to be greater than 12,000 parts per million, there were no palm trees. At Bikar, where the chloride content of the ground water was somewhat lower, there were only a small number of palms bearing nuts that contained very little liquid. Both atolls are uninhabited, and the author knows of no atoll without coconut palms that is permanently inhabited. Thus, in atolls ground water may be more important to man through its control of vegetation than it is as a source of drinking water.

AN ENUMERATION OF THE HYPOTHETICAL ROLES OF ALGAE IN CORAL ATOLLS *

By Maxwell S. Doty
*University of Hawaii
Honolulu, Hawaii*

Our objective here is to enumerate the prospective roles of algae in atoll structure and biology. Essentially this is an enumeration of hypotheses developed from the observations of the Atoll Research Teams insofar as psychological observations were made. It is hoped that this enumeration will lead to testing by future work and that tenable theories of the roles of algae will thereby come to replace these hypotheses.

Flying over an atoll one sees a more or less complete ring of rock just barely submerged beneath the sea's surface. Closer inspection reveals in the water an increase in the size of the fish standing crop, zooplankton population and oxygen production as the atoll is approached and a position inside the lagoon attained. The sea edge of the atoll is solid stone. This edge, from the Carolines and Northern Marshalls to the Tuamotus, is essentially a pink mass, as is much of the water covered, flat, upper surface. The lagoon edge of the atoll ring may be a muddy shore with mangroves, a sandy shore, or a coelenterate coral dominated reef. On the atoll ring there are more or less extensive islands which protrude above high tide line. There is a distinct black area clearly visible in most aerial photographs wherever the above-tide shore is of solid material. The outermost edge of this black area can be taken as high tide line in interpreting aerial photographs. Where not covered with vegetation the surface of these islands, whether sandy, gravel or solid rock, is grey.

Each of the observations related above is apparently rather directly dependent upon algal populations. The hypothetical roles of these algae are of two major kinds, *physiological* and *mechanical*. The *physiological* roles are affected by the action or the utilization of metabolic products. The *mechanical* roles are structural, due to the physical nature of the products accumulating through the physiological activities of the algae. It is our intention here to call attention to these hypothe-

---

* This study was made possible by funds from the Office of Naval Research (U.S.) administered by the Pacific Science Board of the National Research Council as a part of its Atoll Research Program.

Contribution No. 54, Hawaii Marine Laboratory in cooperation with the Department of Zoology and Entomology, University of Hawaii.

tical roles as they are related to the observations on the general appearance of an atoll as described above.

Taking Darwin's hypothesis as a description of the way an atoll forms, we are able to open the first scene of the hypothetical roles played by the algae. The first stage setting is that of an igneous mountain, an island surrounded by an essentially homogeneous sea. The shores of this mountain could be expected soon to become coated with attached algal material. In this algal material there would develop and feed the host of animals to be found in the intertidal area.

The essential limiting salts for algal growth would become concentrated from the passing sea currents and from the rain water flowing down the mountain. Through this accumulation of materials, passed on to the animals that eat the algae, the concentration of the materials required for life would continually increase. This would result in an increasingly dense population. After a time this population is far more dense than that found either in the open ocean or on the newly cooled igneous mountain.

Perhaps largely due to the feeding of fish on fleshy algae below the low level of the tides, the algae that developed there are predominantly calcareous. These algae carry on photosynthesis, making an excess of food material and depositing calcium salts. The story of the reef that develops through the accumulation of calcareous material by the coral organisms, algal and animal, has been told often. But an aspect that has not been emphasized is the continuously cumulative nature of the process. Dead fragments are for the most part passed over the reef edge into the islands or into the lagoon. Continued sea reef edge growth is probably largely by accumulation of new material from the sea. Thus though the role of typhoons is argued, it seems very likely that otherwise atolls continuously increase in mass by the addition of newly accumulated material at their sea margins by the algae.

The primary role of the algae in the Central Pacific must be this removal of inorganic materials from passing oceanic currents. With the energy accumulated by photosynthesis inorganic materials are combined and passed on to other organisms as organic foods. As an example consider *Porolithon onkodes,* the reef covering calcareous alga.[1] For a crustose coralline alga it is peculiar in its ability to thrive in brilliant light and withstand brief exposure to the air. This species is eaten by parrot fish. The parrot fish defecate not only calcareous material but nutrient salts and thus enrich the water beyond the reef. Planktonic algae reincorporate this material into algal cells. Plankton feeders can consume the algae, forage fish and then fish such as the wahoo (*Acanthocybium* sp.) and yellowfin tuna (*Thunus ablunga*) and finally the sharks may receive this material. This food pyramid extends away from the atoll. Thus may be outlined the hypothetical explanation of the increase in populations as an atoll or island is approached.

---

[1] With variations in reef exposure and local topography other species of *Porolithon* may become locally abundant. They rarely become dominant. Rarely a *Goniolithon* appears in numbers but in the situations seen in the Tuamotus only on the reef flat well inshore.

This great increase of fish provides food for the island peoples and, potentially, an income source for them. For example production of whole or ground dried fish might very well be developed as a new source of income to atoll peoples. Production of such a product would be feasible on a family basis and require little material beyond what is already available in any copra producing area.

The legal aspects of oceanic waters have an interesting relationship here. If one is concerned with the fish population near an atoll it would appear that its size would be due to land bound causes. The land owner could cite this in reference to a claim of ownership of the near-shore fish. It is to be noted in this connection that the Polynesian peoples did claim the waters that extended away from the shore of their particular piece of land.

The plankton from an open sea situation would not support the fauna found where it is the animals that dominate the reef: indeed on upwind atoll areas, where the surface currents strike predominantly, coral animals are usually at their fewest. Thus one is inclined to think that the benthic algae must have been the primary organisms of abundance of any new mountain appearing in the ocean. Indeed in Hawaii it is just these sessile algae that are the first organisms to become apparent on new lava flows. One is inclined to suspect it is through their concentration of nutrient salts from the passing sea and the passing of this concentration to locally developing photosynthetic unicells that accounts for coelenterate coral growth and distribution on an atoll-wide basis.

As noted above blue-green algae (or perhaps we should better say blue-green bacteria) grow on and in all surfaces near high tide line. The precise species concerned are considered in the "Reports of the Raroia Atoll Team" in the *Atoll Research Bulletin.* In North Carolina, U.S.A., the blue-green algae so solidly bind the sand that airplanes use these sandy places as practice landing strips. On a coral reef and particularly above high tide line undoubtedly such binding stabilizes the sand bars and binds new sand grains that chance to come to rest. It is through these activities that such a sand bar can be expected to become an island. Particularly in this case the algae have a major role in the establishment of the island as a landmass sufficiently permanent that the climax atoll biota may become established.

They are critical agents in the chain of events leading to the removal of other factors limiting to the terrestrial biota. The accumulation of these from the passing sea current has been discussed above. However, for the sake of argument, with the appearance of algally induced islands two more possibilities arise.

With an increase in size an island on an atoll may come to hold in its interior a body of fresh water. Sea water penetrates the island. This lens of fresh water floats up and down with the tides on top of the sea water and the fresh water in such a situation gradually become mixed with the salt water. Both the freshness and lateral extent of the fresh water lens is regulated by such factors as rainfall, island size, tide range and the permeability of the islands especially near their shores. It has been postulated that the algae play a part in the transformation of the sand at the shore into the beach rock and other atoll rock types.

Birds may use the islands as roosts. This effectively initiates a collection on the islands of nutrient salts from the fishing activities of the birds. Hatheway (*Atoll Research Bulletin*) and Fosberg (see in this volume) have discussed this in some detail in reference to the native vegetation. This seems to be a particularly important factor in the case of phosphate. It is to be noted that the fish phosphate got into the fish as phosphate hypothetically accumulated near the atoll by the sessile algae.

The story of available nitrogen is somewhat different. In part it duplicates the phosphate story. Perhaps in a native climax vegetation with a well developed humus beneath, the birds or bacteria might provide a replacement of available nitrogen lost to the sea. Where there is little or no humus, as in the hurricane-swept Tuamotus, the upper ten centimeters of sand and gravel has a dense layer of blue-green algae that may very well substitute for humus. In the coconut plantations and *Guettarda* groves the soil is largely gravel or nonhumified sand, with sand filling a few decimeters below the surface. Yet there is a root zone well developed.

There is no growth of legumes on these atolls that could account for nitrogen fixation by species of *Rhizobium*. The soil is exceptionally aerobic and of carbonate buffered pH's. There are but few bacteria known (e.g. *Azotobacter* and the *Itersonia* described recently by Derx) that fix nitrogen under these conditions. Bortels, Gerloff, as well as Fogg and others have investigated the nitrogen fixing properties of blue-green algae. It is found that many related to those dominating the

---

[2] *Lithothamnion* is a very unusual alga on the reefs in the Tuamotus and it is not likely to be common on any reef edge in the habitats where ordinarily *Porolithon* is found. The two generic taxa are very distinct, belonging to separate sub-families of the Corallinaceae. Certainly "Lithothamnion ridge" should not be used for the ridge of algal materials which often appears near the seaward edge of sea reef flats.

atoll soils do fix significant amounts of nitrogen. This problem is under investigation at present and preliminary cultural experiments lead us to believe that apparently the soil formed from atolls are significant nitrogen fixers.

The algae cover most of the surface of the atoll and wherever this surface is marine, marine organisms live on the algae. The case of parrot fish feeding on coralline reef formers has already been noted above. Sea urchins at the surface and the countless numbers of boring echinoderms, worms, and other organisms are by their homemaking and feeding habits induced to destroy the algae of the reef and reef flat.

Much attention has been paid to the black zone at high tide line where algae in cooperation with exfoliation must be the principal causes of destruction of the rocks at the seaward edges of the islands. Gastropods of the genera *Littorina, Meloraphe, Tectarius* and their herbivorous cohorts feed on the blue-green algae of the black zone. By their rasping of the algae they remove rock material. The surfaces above high tide on which the algae are growing are softer than those freshly exposed or where no algae are growing. To a certain extent the algae grow into the carbonate rocks. Their pigments diffuse into the rocks and become absorbed. It is most likely that it is the chemical results of these processes that are the causes of the observed softening.

It has been postulated that the softening noticed beneath the black algal coating is an evidence of solution and again of deposition. It seems more likely that it is an evidence of solution aided by the pH variations, especially at night, and the considerable amounts of heat accumulated and thus higher mobilities (but not of carbonate) under the black layer of algal material.

The only reefs seen by the present author to be predominantly coelenterate reefs are those in the lagoons. Such developments are reduced toward the windward side of the atoll and in the more closed atolls. The algae very definitely play a part both in the development and in the death of these animals. Firstly they play a role as the food, directly as phytoplankton or zoozanthellae or indirectly as food for the zooplankton, which in turn may form the food of the coelenterate corals. What is said here is true also of the sea reef corals and those of greater depths.

The edges of lagoon reefs are coelenterate corals at Raroia, elsewhere in the Tuamotus and elsewhere in comparable situations, e.g. at Johnston Island and in Kaneohe Bay on the island of Oahu in Hawaii. Often species of *Pocilopora* or *Porites* form the uppermost surface near the edge as a series of flattened branches condensed behind the reef edge almost into a pavement.

The upward limit of growth for the coelenterate corals on these reef edges seems to be regulated by their tolerance to air exposure. Some algae seem to tolerate air exposure better than the coelenterate corals and grow on the uppermost, often inactive, coelenterate tips just a decimeter or less from the reef edge. This must interfere with the feeding of nearby polyps especially on the side of the algal patches away from the reef edge.

Between the closely arranged coelenterate branches, as the reef extends, circulation must be cut down. In such places algae such as *Rhipilia geppii* grow. They come to fill the spaces between the branches as do such algae as *Zonaria variegata.* This later may extend over the top of the coelenterates a few decimeters in from the edge of the reef so extensively as to mask the coelenterate corals completely. The coelenterate corals become weak structurally and break off; so that in from the edge of the reef there is a lower area, a pool area. In this lower area and on the higher parts of shoreward areas of shore-bound reefs, crustose coralline algae again come to predominate in some localities, especially where the gravel or reef fragments are large.

In any intertidal region, or above on a lagoon shore, the blue-green algae play the same roles as they do on the sea shores already described, but more often on gravel rather than on conglomerate material.

The lagoon bottoms of some atolls are essentially meadows of the green alga *Halimeda.* At Raroia, in the Tuamotus, no dredge haul indicated living *Halimeda* on the bottom. However, there the sides of the reef patches in the lagoon are often clothed with this genus and *Caulerpa.* The latter, as *Caulerpa bikinensis,* is a favorite food of the turtles.

Halimeda is apparently one of the major contributors to the sediments that in turn contribute to filling the lagoon. The calcium salts *Halimeda* deposits are accumulated from the lagoon waters: the other materials filling lagoons come chiefly from outside the lagoon or from alga-smothered dead, or fish consumed, coelenterate corals within the lagoon.

Lastly a word about algae and man. The algae form an important part of the diet of the Oriental, and formerly of the Polynesian peoples wherever available. They are not important apparently in any other way directly, nor are they important to other Pacific people at present nor apparently were they in the past directly. They are, however, prospectively of great importance to these people as a major primary cause of their food and land.

FACTORS INFLUENCING THE DISTRIBUTION OF CORALS ON THE REEFS OF ARNO ATOLL, MARSHALL ISLANDS[1]

By Robert W. Hiatt
University of Hawaii
Honolulu, Hawaii

Introduction

This paper presents a small but significant facet of a broad investigation into the marine ecology of Arno Atoll, Marshall Islands, which, in turn, is a portion of a comprehensive study of the atoll by a team of scientists representing several disciplines including geology, geography, hydrology, climatology, marine ecology, botany, entomology, agriculture, vertebrate zoology, and anthropology. The objective of the integrated investigation was to provide a broad basis for learning the nature of life processes in these self-contained microcosms so that a coherent and understandable picture of a limited tropical total environment would emerge.

Although the writer was engaged in studying many ecological aspects of the reef environment about the atoll, one compelling feature was the recognition that, regardless of the geographical location about the atoll, the reef tracts were roughly zoned parallel to the reef margin. Oftentimes the zones were characterized by certain organisms which dominated the area; elsewhere the parallel bands were depositional flats, or frequently were solid and pavement-like. In any case it was apparent that the distribution and abundance of virtually the entire assemblage of organisms which dwell upon these coral reefs were intimately associated with and influenced by the various reef facies present. Because of these relationships a systematic collection of data along transects across both the sea and lagoon reefs was undertaken to interpret more precisely the underlying causes of zonation. During this study very wide fluctuations in salinity, far greater than any reported previously in the literature, were discovered. Wide differences in salinity were noted between high and low tides and between the sea and lagoon reefs. Since these variable salinity gradients appeared to have no direct relation to rainfall, it was obvious that the only source of fresh water could be the ground-water held within the islands and islets.

---

[1] Contribution No. 44, Hawaii Marine Laboratory, in cooperation with the Department of Zoology and Entomology, University of Hawaii.

By working closely with the hydrologist of the party an explanation of this phenomenon became apparent, and it is this environmental factor which is analyzed in greatest detail in this report. However, because zonation on coral reefs doubtless results from the interaction of many environmental factors, several of these which are considered important on Arno reefs are stressed.

Only corals are used as key animals in defining various aspects of zonation on these reefs because they are fixed in position and each species possesses a relatively narrow ecological valence. Thus the distribution of certain types of corals may be used as an indication, of limiting or inhibiting factors present across the reef tract. Important too is the fact that they may be considered quantitatively, both as regards species and population densities.

LOCATION AND GENERAL DESCRIPTION OF ARNO ATOLL

Arno Atoll, lying in the southern Marshall Islands at approximately 172°E. and 7°N., is in the northeast trade wind belt and for most of the year in the path of the North Equatorial Current. During the summer months the Equatorial Counter Current swings northward, deflecting the North Equatorial Current, and probably influences the atoll with its eastward flow. Ocean water temperatures do not fluctuate more than 1 degree above or below 28°C. The temperature, clarity and agitation of the surface waters are optimum for coral growth, but the planktonic food supply, despite the apparent favorable position at the convergence of major ocean currents, is less than in areas further to the southwest, so coral growth is somewhat below the potential maximum, yet must be classified as flourishing.

Arno is rectangular, rather than a circular, atoll with two extensions or "horns," one extending to the north about 5 miles from the north center of the rectangle, and the other extending about 7 miles northeastward from the east corner (Fig. 1). The total area enclosed by the seaward reefs and lagoons is about 147 square miles. The surface reefs cover about 16 square miles and on them 133 islands and islets form about 5 square miles of dry land. Two deep passes and 3 shallow ones interrupt the continuous seaward reefs around the atoll. The total circumference of the seaward reefs is about 65 miles.

The islands and islets have been built by the forces of winds and waves from materials derived from the living reefs. They are accumulations of loose material partly held together by a framework of beach conglomerate to seaward, beach sandstone lagoonward and interior island sandstone. Surface processes and changes are everywhere in evidence about the atoll, and frequently vast changes are observed, primarily on the lee side of the atoll, which have resulted from occasional great typhoons.

Reef types at Arno Atoll have been briefly described by Wells (1951) and classified by him following the scheme for designating seaward reef types set forth by Tracey, Ladd and Hoffmeister (1948). These are shown in Figure 1.

The lagoon reefs are less continuously developed than the seaward reefs. The best development on the lagoon side occurs along the west, south and north sides of the atoll. The only sizeable development of leeward lagoon reefs on the north or windward side of the atoll is in the vicinity of the two deep passes, Tutu and Tak-lib. Coral knolls or patch reefs are numerous in the lagoon and Wells surmises that their distribution is less than fortuitous, inasmuch as the clusters appear to bear some relation to the passes through the windward rim of the atoll.

The dominant type of seaward reef (Type 1A), characterized by strong grooves on the seaward slope which do not cut the low algal ridge at the margin, extends almost uninterruptedly from the west side of the North Horn southward around the lee side of the atoll to the eastern edge of the East Horn. The inner half or more of the reef platform is flat, almost barren, and supports coral growth only in occasional depressions. Blanketing this reef flat is an extensive growth of a brown alga (*Microdictyon okamurai*) on the fronds of which live vast quantities of the foraminiferan *Calcarina*. Here and there are many large, securely attached rock oysters (*Chama*). Wells has termed this zone *Calcarina-Chama*. On the gradually sloping outer third of the reef flat near the upper ends of the grooves stubby colonies of *Pocillopora* dominate. In the surf zone *Pocillopora* gives way to *Acropora* (*A. pectinata, A. digitifera*, etc.). Other prominent coral genera here are *Astreopora, Porites, Millepora* and *Favites.*

The exposed windward reef tract is characterized by Type IB, which has a relatively high, prominent algal ridge cut frequently by grooves. The broad, rocky flat supports much less *Chama* and the *Microdictyon-Calcarina* association is less evident. Toward the outer slope *Acropora cuneata* occurs in shallow depressions, but even this species is not abundant. One is impressed with the very striking difference between the horizontal zonation of the windward reefs of Arno and those of Bikini Atoll. The corresponding reefs at Bikini are much wider and are characterized by broad outer and inner *Heliopora* zones which contained rather large subcircular masses of this blue alcyonarian in the form of micro-atolls (Ladd, Tracey, Wells and Emery, 1950).

The third seaward reef type (Type IIA) in which the grooves are weak and the margin is smoothly scalloped was found only in a small area at Ine Anchorage (Fig. 2). This area is distinctly zoned by corals, the dominant genera of which are shown in Figure 4. The inner portion of the reef flat is barren and exposed for a long period at every low tide. Extending seaward is a broad band thickly covered mostly with a pure stand of *Montipora gaimardi*, replaced here and there with patches of *Acropora hebes* or alcyoniid "soft corals" (*Lobularia krempfi*). A few micro-atolls of *Synaraea, Leptastrea* and *Porites* occur at random. During low tide in this zone the depth varies from exposed surfaces to shallow depressions as deep as 15 inches, and the water is undisturbed by swells or waves of translation. The seaward limit of this band is at about the inner extent of the ordinary low tide waves of translation. From this point to the reef margin *Acropora* dominated, especially species of the corymbose *A. pectinata* type. This is the zone of the richest variety of corals and associated animals on the reef flat and, unlike other seaward reef types, calcareous algae are relatively very unimportant. At least 33 genera of scleractinians and hydrozoan corals were collected in this zone, but *Acropora* accounts for about 90 per cent of all the colonies. On the steep slope over the reef edge and in the re-entrants along the edge an even greater variety of corals was found, numbering at least 90 species. Moreover, this area supported the most flourishing stand of corals, dominated by the majestic pedestal colonies of *A. reticulata* which began about 6 feet below low tide level, where the water was only slightly agitated by gentle swells, and extended down to about 60 feet, below which level *Porites* dominated the slope.

Description of the Study Areas

Seaward reef transect

The position of this transect is seen in Figure 2. The most prominent facies present along the transect have been described earlier in the description of the Type IIA reef present only at Ine Anchorage, and the dominant organisms are indicated in several text-figures depicting the zonal distribution of both physical factors and corals.

At the position of the transect the reef tract is about 450 feet broad, and is entirely covered at high water spring tides by about 4 feet of water. At mean low water it is uncovered to the boundary between quadrats 5 and 6, some 200 feet from the beach (Fig. 4). A few large, shallow tide pools are present in the barren rocky flat extending from the beach to quadrat 3, a distance of about 75 feet. Several boulders in one of these pools provide sheltering crevices in an otherwise highly exposed substrate. From quadrats 3 to 6 there are innumerable shallow basins and channels which hold water when the general level of the rock surface is exposed. Quadrats 7 to 9 always contain water above the average reef rock level and, in addition, contain many shallow to deep sandy-bottomed channels thickly lined with coral colonies. Quadrat 9 is bordered on one side by a narrow re-entrant channel. The reef margin, included in quadrat 10, is elevated slightly and exposed at ordinary low water. The ocean swells, however, continually sweep this low coral ridge so that it is never exposed for more than a few seconds at a time. Very few depressions or channels dissect this region and the coral heads on it are sparse, low and rather heavy. The seaward slope is precipitous, descending nearly vertically to about 35 feet, then continues downward at approximately a 70 degree angle with the water surface. Re-entrant channels are common and border both sides of quadrat 10.

Ine Anchorage is in the lee of Ine Island, thus the water over this transect was rarely influenced by the usual northeast trade winds. Wave action, particularly during low tides, was virtually absent because of the protection afforded by Stony Point to the east of the transect and because of the steep slope of the island to seaward in this location. Ocean swells from the south moved onto the reef at an incident angle because of the northwest-southwest reef margin at the Anchorage. At low tide they produced low, gentle waves of translation which flowed over the reef flat toward shore as far as quadrat 6. At high tide, particularly when the swells were extensive, waves broke just shoreward of the reef edge and strong waves of translation swept onto the beach, carrying small boulders and gravel to and fro across the inner barren zone and up the rather steep slope of the beach. During such periods considerable suspended material made the water turbid, but it settled out quickly during quiet periods.

Lagoon reef transect

Because of time limitations the very broad windward reef tract on the lagoon side of Ine Village was passed over in favor of a narrower reef tract at Makin Islet (Fig. 3). This transect was approximately 400 feet in length, running from the boulder and beachrock shore line to a depth of about 40 feet on the lagoonward slope. At mean low water approximately one-half of the reef flat was uncovered. Inshore the flat, rocky substrate was sprinkled with large and small pieces of beach conglomerate. These provided virtually the only seclusion for the intertidal fauna. Sandy bottom became the dominant substrate at about 100 feet from shore.

Scattered about the outer 200 feet were clustered coral heads which, from the point of deflection from the reef flat to the lagoonward slope, were growing from the surface of giant, irregular columns of dead corals. These were replaced at approximately 25 feet in depth with a thicket of *Acropora formosa,* which continued downward beyond vision.

The extreme clarity of water here, coupled with the presence of sandy substrate, the surface layer of which was composed of exceedingly fine particles which remained suspended for hours after being disturbed, denoted an area infrequently disturbed by wind or wave. There is no elevated coral or algal ridge at the margin, differing in this respect from the broader windward lagoon reefs which are often subjected to winds and crashing waves. The delicate growth form of the corals add further testimony to the quiescent physical state along this transect.

Review of the Literature

Horizontal zonation of corals and other reef flat facies have been observed and described in greater or lesser detail by almost every geologist and biologist who has studied coral reefs, but few have given more than passing attention to it. The more important general studies of zonation on coral reefs are those of Wood-Jones (1912) on Cocos-Keeling Atoll, Tracey, *et al.*, (1948) and Ladd, *et al.*, (1950) on reefs of Bikini Atoll, northern Marshall Islands, and Wells (1951) at Arno Atoll in the southern Marshall Islands. Wood-Jones pointed out that on Cocos-Keeling Atoll various forms (not species) of corals had a fairly defined site of election; but in spite of this their distribution was capricious, there being no particular distinction between lagoon corals or sea reef corals. The facts that particular species might be found both on the lagoon and on the sea reefs, and that environmental modification of corals provided many growth forms of a single species led him to suggest that the distribution of atoll corals is a distribution of types, and *not of species* (italics his). Moreover, he recognized that the unfavorable conditions of crashing surf at the reef margin outweighed the assumed advantages of better aeration and more abundant food so that in this zone living coral reached its minimum of colonies as well as of species. At Cocos-Keeling the corals increased in number and variety toward the sheltered lagoon waters. A general survey of the reefs at Bikini by Tracey, *et al.*, resulted in a preliminary zonal analysis of the seaward reef and a classification of main seaward reef types based upon the characteristics of the marginal zone. Later more detailed analyses were presented by Ladd, *et al.,* whose consideration of the distribution of the coral fauna included the lagoon floor, coral knolls or patch reefs, the lagoon reef flat, the seaward reef flat and the seaward slope down to a depth of 800 feet. No suggestions concerning the relation between environmental factors and the distribution of corals were made. Coincident with the detailed study of portions of the reefs of Arno reported herein, the broad aspects of zonation there were examined and reported upon by Wells.

The most significant detailed studies made on restricted areas of coral reefs are those by Mayor (1918, 1924) on the fringing reefs of Maër Island, on the northern end of the Great Barrier Reef, and in Tutuila, Samoa; that by Baker (1925) on a fringing reef of Gaua Island in the New Hebrides; and that by Manton (1935) on reefs of the Low Isles, a Low Wooded Island type just north of Trinity Opening in the Great Barrier Reef.

The extensive studies at Maër Island and on Aua reef, Tutuila, by Mayor have provided a wealth of detailed ecological data on the distribution of corals. Unlike Wood-Jones, Mayor concluded that each species of coral thrives best at some definite distance from shore and found but three genera (*Porites, Pocillopora* and *Goniastrea*) which extended clear across the reef flat at Maër, and only one so distributed at Aua (*Pocillopora*). Each of the common corals was found to attain a well-defined maximum in number of heads at some definite distance from shore and declined in frequency both shoreward and seaward. In general he found the maximum number of coral heads some distance behind the edge of the reef in relatively quiet water, but the greatest variety of corals was found closer to the outer edge. The distribution of corals on both reefs was somewhat similar, with zonation well established. However, most of the colonies at Maër consisted of but four genera (*Porites, Pocillopora, Acropora* and *Seriatopora*), while at Aua reef *Psammocora* replaced *Seriatopora*. Mayor concluded that the factors chiefly responsible for the mode of distribution of the various species of corals at Maër Island were, in the order of their importance, (1) temperature, (2) silt, (3) mechanical effects of moving water, and (4) the struggle for existence between the various species of corals. In the New Hebrides, coral growth appeared most abundant near shore where *Montipora ramosa* and *Goniopora* were dominant, with *Montipora* covering about 85 per cent of the reef surface. Farther out other genera (*Porites, Acropora*) dominated certain areas up to about one-fourth mile from shore, and from that point seaward coral growth was comparatively sparse. The traverses across reefs of the Low Isles by Manton cannot be compared with those previously outlined because of the rather different form and position of the reef tracts examined. Coral growth here was most abundant in the deeper part of the Moat and on the seaward slopes, with zonation evident only on the latter. Factors considered to be most influential in the distribution of corals on Low Isles were (1) level of the substratum in relation to that of low water and to the maximum duration of low tides, (2) the ranges of temperature and salinity of the water, and (3) the nature and amount of the sediments which are deposited and which may lie undisturbed on rocks and corals.

All those investigating zonation of corals on reefs concur that no one environmental factor is solely responsible, but there is no concordance concerning the ranking in importance of those most influential. The more important studies of the deleterious effect of silt and the varying ability of different corals to remove it from the surface of the polyps were made by Wood-Jones (1912), Mayor (1918, 1924) Edmondson (1928), Manton (1935), Umbgrove (1947) and Wells (1951). In general, corals confined to the seaward areas are less able to withstand suspended silt or a covering of silt than those characteristic of the mid-reef flat and inshore areas. Moreover, the differences observed by contrasting the coral species and their distributional patterns on seaward vs. lagoonward reefs are believed to result mostly from finely particulate silt in the lagoon and larger, sandy sediments on the more turbulent seaward reefs.

Exposure to air is an inhibiting factor to virtually all corals, yet a certain few exceptional species are ubiquitous on the shoreward portions of reef tracts which are elevated slightly above the level of mean low water. *Montipora ramosa* appears to be the dominant type in exposed inshore areas in the New Hebrides, Low Isles, Maër Island, and in the East Indies; indeed, it thrives so well in this location that it has given rise to the designation "*ramosa* facies" by Umbgrove (1947). At Arno Atoll *M. gaimardi* occupies a similar location (Wells, 1951). A few species of corymbose *Acropora*, particularly *A. hebes*, are also common constituents of the fauna at Arno in areas exposed for brief periods each day. Vaughan (1916) found that the ability of corals to withstand exposure to air is a function of the porosity of the skeleton, the species with the more porous surviving longer than those with the denser skeletons. Thus porous types, such as *Montipora* and *Acropora*, with their bases in water are able to survive because the water is elevated through the skeleton by capillarity. Experiments by both Mayor (1918) and Edmondson (1928) on compact and cavernated types exposed to direct sunlight, some with and some without their bases immersed in water, corroborated Vaughan's earlier conclusions.

Most investigators consider the temperature gradient across a reef to influence the distribution of corals. Solar radiation causes greater temperature fluctuations in shallow inshore waters than it does at the reef edge, thus excessively high temperatures during certain days of the year could restrict inshore waters to a few hardy species (Mayor, 1918, 1924; Wells, 1951). Some experimental evidence presented by Mayor (1918) indicates that certain genera restricted to the edge of the reef were killed by temperatures not exceeding 37° C., yet inshore types thrived until water temperatures rose well above 37° C. On Hawaiian reefs Edmondson (1928) was unable to secure such clear-cut correlation between temperature tolerance and the position of corals on the reef.

Generally speaking dilution of sea water has not been considered one of the critical limiting factors in the distribution of corals except for inshore areas and for periods when low tides, torrential rains and calm seas combine to kill corals over considerable areas. Vaughan (1916), Mayor (1918) and Edmondson (1928) found that most corals were not adversely affected in water having a salinity of 75 per cent of normal sea water, but that greater dilutions would kill corals within a few hours. Mayor could find neither a higher concentration of sea water at low tide due to evaporation nor a dilution of sea water due to an influx of spring water from the shore at Maër Island. This latter situation may have resulted because his visit coincided with the end of a long dry spell. Thus, the record to date would imply that fluctuations in salinity are not of paramount importance in the zonation of corals except for those well inshore.

A factor long presumed to be significant in the distribution of corals, but one which has been neglected except for the work of Verwey (1931), is available oxygen. Working both on oxygen consumption of individual corals and of sections of reefs he concluded that the oxygen demands would necessitate considerable water motion, and where such movement is absent or slow reef growth may be depressed.

The record thus far gives us very little information as to what extent the distribution of corals may be influenced by competition between species for available space and food. Mayor (1918) suggests that in the surf zone where coral heads are small and not densely crowded, their struggle for existence is mainly with the sea as an adverse environment and not with one another; whereas in the less agitated water where the environment is favorable and the coral colonies are crowded, there is abundant evidence of a severe struggle between various forms for dominance, and the kinds that can survive are few. Manton (1935) recognizes the possibility of such an effect because the thickly growing heads of *Acropora* appear to discourage the establishment of other species among them.

Previous studies thus indicate that not only do several factors influence the distribution of corals on reefs but that these factors themselves are variable, exerting their limiting or inhibiting effects on different sections of the reef tract from the shore to the reef's edge. Factors affecting inshore distribution, in order of rank, appear to be exposure, temperature and salinity; those affecting mid-reef areas are thought to be sedimentation and interspecific competition; while at the reef's edge the impact of waves seems predominant. Differences in the distribution of corals on windward and leeward reefs are attributed to sedimentation and the turbulence of water.

Acknowledgments

The writer was a participant in the 1950 SIM (Scientific Investigations in Micronesia) Project of the Pacific Science Board of the U. S. National Research Council. This project was supported by funds granted to the National Academy of Sciences by the Office of Naval Research, and the field work was carried out with the active assistance of the Navy Department, the Military Air Transport Service, and the officials of the Civil Administrative Staff of the Trust Territory of the Pacific. The University of Hawaii provided technical assistance for working up voluminous data. Miss Ernestine Akers of the Pacific Science Board aided in many ways.

Much of the value in this project emerged by cooperative assistance with colleagues in other fields. Thus to Dr. Donald W. Strasburg, who assisted in the marine studies, I owe a great debt of gratitude. Doak C. Cox, hydrologist; John W. Wells, geologist; and Leonard Mason, anthropologist, were most helpful in providing useful information. Without the services of James Milne and Konto, native interpreters, our work would have been far more difficult and less complete.

Methods

The seaward reef transect was a strip 50 feet wide from the shore to the slope over the reef margin. At intervals of 50 feet along the transect rock mounds were erected so that the area could be examined in quadrats 50 feet on a side. The lagoon transect was laid out similarly except that the quadrats were 100 feet on a side.

In each quadrat estimates were made of the amount of reef surface covered by the dominant corals, and a map was constructed showing their distribution. Specimens of each coral type in each quadrat were collected and prepared for taxonomic study.

Measurements of water temperature were taken in the center of each transect at both high and low tides at intervals throughout the summer period. Whenever extreme weather conditions prevailed sea reef and lagoon reef temperatures were taken so that data during extreme as well as normal weather conditions could be considered. All temperatures were taken at the level of coral growth by holding the thermometer on the tops of coral heads and reading it underwater with the aid of a diving mask. Temperatures in quadrat 11 on the sea reef slope and in quadrat 4 on the lagoon reef slope were measured at a depth of 20 feet by diving down with the thermometer and holding onto coral heads for one minute, then reading the instruments before rising to the surface.

Water samples for chlorinity determinations were taken in the center of each transect at the same depth and time as the temperature readings were made. Chlorinity analyses were made in the field with a Wheatstone conductivity bridge which was calibrated against samples of sea water titrated with silver nitrate solution. Properly preserved samples were returned to Honolulu for accurate determination under better laboratory conditions, after which all field determinations were corrected.

Accurate determinations of levels of the sea reef platform, of the tops of coral heads and of the adjacent beach were made with an alidade; these levels, in turn, were related to the datum which was 0.0 on a staff attached to a portable tide gauge fixed on a re-entrant channel at the margin of the reef. Datum level was 4.1 feet above mean sea level, 1.9 feet above mean low water, and 1.9 feet below mean high water.

The tides were measured at the margins of both the lagoon and sea reef by portable, recording tide gauges supplied by the U. S. Coast and Geodetic Survey. From these brief records the U. S. Coast and Geodetic Survey computed the tidal relationships by referring all elevations to mean sea level in the ocean. The following data were computed:

	at ocean	*at lagoon*
Mean high water	1.90	1.93
Half tide level	0.00	–0.02
Mean sea level	0.00	——
Mean low water	–1.90	–1.97
Mean low water spring	–2.75	–2.82

Because climatic data taken for a period not exceeding two months is very inadequate to indicate changes even through a single season, the data are fragmentary. These, however, have been correlated with other scant but longer term records on the neighboring atoll of Majuro so that an indication of the hydrologic factors in the climate of Arno can be estimated. The mean monthly rainfall recorded from July through November at Ine Village was 17 inches, equivalent to an annual rainfall of over 200 inches. Daily rainfall during the period of observation ranged from nil to over 4.14 inches. Most of this rain came in sudden intense rainstorms. No relation of rainstorm frequency to time of day was noted. The air temperature during the period of operation of the weather station ranged from 73° to 90° F. with a maximum daily range of 19 degrees and a common daily range of 10 to 12 degrees.

Because this paper emphasizes the relationship between salinity gradients on the reefs and ground-water, a detailed account of essential ground-water principles appears later in the section on salinity under "Factors Influencing Zonation." The hydrologist at Arno, Doak C. Cox, made detailed studies on the ground-water and found it to function as a typical Ghyben-Herzberg system. Ground-water characteristics were measured in various ways, including recording gauges, in land surface depressions, retting pits, taro pits and wells.

Descriptive Zonation of Corals

Only three major zones, dominated by two prominent genera, exist on the seaward reef transect. These are shown in vertical section along with Figures 4, 6, 7, 8 and 10. Rather stunted heads of *Montipora gaimardi* are first found in the seaward portion of quadrat 3, approximately 75 feet from the edge of the sand beach. In quadrat 4 the abundance of *M. gaimardi* heads increases greatly with a few scattered representatives of *Acropora hebes, A. pectinata* and *Porites lutea* growing in shallow pools. The area most completely covered by *M. gaimardi* occurs in quadrat 5, and the species gradually disappears seaward in quadrat 7. It is easily the dominant species in quadrats 3 to 6 covering 150 feet along the transect. *Acropora* gradually replaces *Montipora* about midway in quadrat 6 and thoroughly dominates the coral growth from this point to the reef margin, about 250 feet further. On the upper 20 feet of the steep reef slope *Pocillopora* is dominant. This merges below with a mixed zone reaching downward to about 35 feet in which no type is outstandingly conspicuous. From this depth down to about 55 feet the large pedestal colonies of *A. reticulata* flourish in the relatively calm water and clearly dominate the area. Below 55 feet these colonies give way rapidly to a rather thick coral cover in which *Porites lobata* is most common.

That the number of kinds or species of corals increases steadily toward the seaward edge of the reef at Arno is easily seen in Figure 4. Compared to coral distribution described in various other reef areas, this pattern of species density differs from that usually encountered. Ordinarily the greatest species density has been observed at the point where the surge dies out in ordinary weather (Mayor, 1918, 1924; Baker, 1925). This would correspond to quadrat 9 at Arno, which contains fewer than three-fourths the number of species found in quadrat 11 located down the steep outer face of the reef platform. In another aspect of the distribution of corals, the Arno reef agrees with studies made elsewhere in that the fewest species occur inshore, but species density increases consistently seaward.

Quite a different picture is presented when considering population density along the transect. The *Montipora* zone, covering quadrats 3 to 6, had by far the greatest area covered by growing corals. Only scattered bare areas existed in this region where approximately 75 per cent of the reef flat supported a flourishing growth of *M. gaimardi.* This situation appears to be a replicate of that reported by Baker (1925) in the New Hebrides and by Mayor (1918) at Maër Island, where *M. ramosa* was the exceedingly abundant species exposed by moderately low tides near shore. No other area within the transect even approaches the inshore portion as regards the density of the stand. Heads of *Acropora* and associated genera comprise the next most dense thickets in quadrats 7 to 9 just at the inner edge of the normal surge zone where water is always present. Fewest heads appear in quadrat 10 which contains the elevated reef margin frequently subject to the impact of breaking waves.

The distribution of corals on the lagoon transect was very different from that of the seaward reef. No thick stands of corals occurred; instead, individual colonies or clusters of them arose from a sandy substrate underlain with coral boulders or, in deeper water toward the margin and down the slope, were attached to the sides and tops of massive columns of *Porites andrewsi.* Corals did not flourish on the inner half of the reef flat and were abundant only in quadrats 3 and 4. The margin of the reef marked the boundary between quadrats 3 and 4, so corals in quadrat 4 were characteristic of the lagoonward slope of the reef tract. On the inner half of quadrat 3 a mixed zone occurred in which no clearly dominant genera emerged. Rather, *Acropora, Stylophora, Astreopora,* and *Seriatopora* heads were present in about equal numbers. As the water deepened to approximately 4 feet at mean low water near the outer boundary of quadrat 3, the massive irregular columns of *P. andrewsi* clearly dominated the scene and very few colonies, aside from pedestal colonies of *Acropora* in the sand, grew from any other substrate. Heads of *Acropora* and *Astreopora* growing on dead portions of the *P. andrewsi* columns were dominant. Down the reef slope from 10 to 25 feet pedestal colonies of *A. reticulata* were very abundant, interspersed with loosely branched, erect colonies of *Hydnophora* and *A. formosa.* Below this depth thickets of *A. formosa* flourished and apparently extended across the entire floor of the lagoon.

Unlike the distribution of species across the sea reef the kinds of corals in the lagoon transect appeared to show no zonation within the section of the reef which was not completely inhibiting to coral growth (Fig. 5). Species density on the lagoon reef was generally less than on the sea reef, due almost certainly to the comparative lack of suitable substrate for attachment of colonies. Nearly every coral boulder sufficiently large and stable to support a living colony was occupied. Population density, however, did vary, with the bulk of the individual colonies located in quadrat 3, just shoreward from the margin of the reef. This area also had a slightly greater number of species present.

It is apparent that corals on the sea reef flat and outer slope are zoned both as regards kinds and numbers of colonies, whereas those on the lagoon reef flat show virtually no zonation as regards kinds and but little zonation with respect to head density. However, zonation of kinds of species is evident on the lagoon reef slope.

Factors Influencing Zonation

Exposure

Relationships of levels of the reef rock platform, the top of coral heads and the gross aspects of zonation on the sea reef transect to the tidal periods and levels are shown in Figure 6. The entire reef platform, including the corals, is covered at mean sea level. When the tide is at this level or above swells rarely peak up and break at the reef margin, but instead sweep on shoreward to break first about quadrat 6. At mean high water the waves rarely break before reaching quadrat 2 or 3, consequently the heavy impact is spent either on the barren reef rock or on the sand beach. During periods of inclement weather breaking waves may occur at any place from the margin inward.

At mean low water the shoreward half of the reef from midway in quadrat 5 is exposed, thus for several hours each day this portion of the reef is without water except for that held in shallow depressions and pools. It will be noted in Figure 6 that from just behind the reef margin to about quadrat 6 the top two inches of most of the coral heads will be exposed. From this point to quadrat 3 entire coral heads will be exposed unless they are situated in depressions. The rather sharp break between the inshore *M. gaimardi* zone and the seaward *Acropora* zone also occurs at this point, thus implying that exposure is a limiting factor of considerable importance for types other than *Montipora*. *M. gaimardi*, like *ramosa*, is able to withstand long periods of exposure whereas *Acropora* is more severely limited in this respect, permitting *Montipora* to flourish in a thick, nearly pure stand shoreward from the inner extent of ordinary low tide waves of translation. Close inspection indicates that these *gaimardi* colonies actually have their bases covered with 1 to 3 inches of water because they are located in very shallow depressions. Vaughan (1912) first suggested that cavernated forms like *Montipora* and *Acropora* could survive exposure to air and sun for long periods so long as their bases were in water, whereas compact corals were unable to withstand such exposure. Spongy forms, provided their bases are immersed in water, can draw up water by capillary attraction so that they retain their internal moisture even though exposed to the desiccating effects of the mid-day sun. Vaughan (1916) noted later in the Bahamas that species with porous skeletons also withstood greater desiccation than other types, and Mayor (1918) described a similar situation on Maër Island reefs. Mayor, and later Edmondson (1928), put this hypothesis to experimental test and fully corroborated the assumption made from observations in the field. The distribution of *M. gaimardi* at Arno may be interpreted as being influenced principally by the amount and duration of exposure to the direct rays of the sun. However, other factors, for example, temperature and salinity, also appear important in influencing this distributional pattern and certainly act in concordance with the tidal cycle.

Because mixed, semidiurnal tidal rhythms are characteristic on Arno shores, the distribution of many intertidal and subtidal species is undoubtedly influenced by "critical tide factors" as described for the Pacific Coast of the United States by Doty (1946). Although marigrams of Arno tidal features are not available over extensive periods, it is evident that successive high tides or successive low tides are often of appreciably different heights. As regards high tides, there is an alternation of higher high water with a lower high water, followed in turn by another higher high water, etc. Successive low tides show similar alternation. As might be expected the elevational aspects or variations of tide factor activity seem to be associated most frequently with the highest or lowest elevations of these four tides, and Doty (1950) has designated eight critical factors accordingly. These factors may, of course, be critical for a particular day, or for any period, depending upon the organisms and the modifying factors influencing tidal levels.

The true aspects of tide factor activity are associated, for corals at least, with effects on them of the duration of a single submergence or emergence at particular levels. For example, should the maximum height of lowest lower high water not exceed 0.5 feet then the corals shoreward from quadrat 6 would be exposed or have only their bases in very shallow water for a period as long as 17 hours, whereas corals below this level would be exposed or would be in very shallow water only for a maximum of about 8 hours. Along the western and eastern coasts of the United States rather sharp breaks in the vertical distribution of sedentary intertidal organisms have been found to coincide with the predicted levels for these tide factors. Exposure (i. e., desiccation) alone has not been found so important a factor in zonation as was generally believed, but ancillary factors which can exert their greatest influence during periods of exposure, e. g., temperature elevation during clear sunny periods, rain or other sources of dilution, freezing, etc., have been suggested as most important (Doty, 1950). The extent to which various factors may act in accord with exposure will be discussed in subsequent sections of this paper.

A large number of micro-atolls occur in channels or depressions in quadrats 5 to 7. Most, if not all, of these have been formed by the killing and slight excavation of the center of colonies of *Porites* and *Synaraea* which grow up above mean low water. Despite the fact that the formation of micro-atolls is usually attributed to effects of sedimentation, influences of this sort have been unimportant in their formation at Arno. Rather, unfavorable environmental factors related in some way to periods of exposure have regulated the formation of these micro-atolls. Nothwithstanding the vigorous growth on the part of these compact corals, they are unable to elevate their colonies above the water level of the channels and pools. The edges, however, grow outward as thick as the depth of the pool. In many cases the colonies are 3 to 5 feet in diameter. This type of micro-atoll formation is precisely the same as that on the windward Bikini reefs (Ladd, *et al.,* 1950) and reefs in the Talaud Islands, East Indies (Kuenen, 1933).

No coral species in the lagoon occupied a comparable location to *M. gaimardi* on the sea reef. During spring lows the tops of large colonies of *Porites lutea* and *Pocillopora eydouxi* were exposed, but only for brief periods of time. Thus exposure to the direct rays of the sun appeared to be an inhibiting factor for species of corals occupying the lagoon reef.

Water movement

Water transport and turbulence varied greatly between the sea reef transect and that on the lagoon reef, even though both were rather protected. Water movement is evidently an important factor in zonation on the sea reef particularly as regards (1) the sharp break in species density noted between quadrats 6 and 7, (2) the large number of heads in quadrats 8 and 9, (3) the shape of the heads at the reef margin in quadrat 10, and (4) the distribution of the enormous pedestal colonies of *A. reticulata* on the steep seaward slope.

The boundary between quadrats 6 and 7 marks the inner extent of the waves of translation during normal low tides. Shoreward the water is confined to pools and shallow depressions; seaward it is constantly being replenished with each succeeding wave. The favorable effects of moving water on corals such as continued high oxygen content (Verwey, 1931), replenished planktonic food supply, maintenance of rather high salinity values and the maintenance of temperature close to that of offshore waters, seem to be reflected in the greater number of kinds present. High population densities in quadrats 8 and 9 reflect all the favorable situations mentioned just previously, with an additional one—greater depth of water. The greatest turbulence occurs in quadrat 10 which includes the reef margin. Except for numerous channels the reef is elevated at the margin (see Fig. 6) thus subjecting coral heads both to brief exposure and to rather heavy wave action. The elevated areas are sparsely covered with a few hardy, heavy colonies of *Acropora* and *Pocillopora*, but the channels are thickly clothed with many species. The upper 15 feet of the outer slope, which is strongly influenced by the surge, is heavily clothed with a great variety of species, but below the surge zone the delicate pedestal colonies of *A. reticulata* grow vigorously down to a depth of about 60 feet.

Waves of translation are absent on the lagoon transect; the water there just rises and lowers quietly with the tide. There is no zone of breakers and no surge. Thus we would not expect sharp breaks in either species or population density. Moreover, since the surge is absent, pedestal colonies of *A. reticulata* begin at a depth of 5 feet near the margin of the reef and flourish downward to a depth of about 25 feet. Striking differences in water movement and turbulence on the two transects at Arno is therefore quite evident, with zonation on the sea reef influenced by them, whereas no distributional patterns related to these factors are apparent on the lagoon reef transect.

Silt

It has been stated elsewhere in this paper that the sea reef in the vicinity of the transect is virtually free from silt. During high tides when turbulence is greatest over the reef rather heavy particles of sand are suspended in the water, but these settle out very rapidly as the tide ebbs. Thus silt is a negligible factor in the distribution of corals and coral types on the sea reef transect.

A very fine, whitish silt covered the bottom on the lagoon reef transect, and it quickly rose in a cloud if disturbed. In normal weather the area was sufficiently protected so that suspended silt was largely absent. However, shifts in wind direction during storms would certainly stir this area making silt an inhibiting factor to those corals unable to withstand it. The bases of coral heads present were all dead and the colonies themselves were rather widely scattered because sand and silt covered the bottom, leaving few boulders or dead coral heads exposed for attachment.

The most abundant heads in quadrat 3 belonged to the following genera, in order of abundance: *Seriatopora, Stylophora, Acropora, Astreopora, Goniastrea* and *Montipora.* Of these *Goniastrea* and *Acropora* have been previously shown to be very capable of withstanding considerable siltation (Mayor, 1918, 1924), but *Seriatopora* has therefore been believed to have very little resistance to sedimentation. None of the other genera have been examined experimentally as regards their resistance to silt. It is evident that much more experimental work must be done before silt as a factor in zonation of corals can be seriously considered. Especially is this so when many outstanding investigators have stated that silt is the most important factor in limiting or inhibiting coral growth (Wood-Jones, 1912; Manton, 1935; Umbgrove, 1947). Because of the conflicting reports on comparative experimental studies on the effects of silt on coral growth, it is impossible to make adequate analyses of the differences in kinds of corals found on the lagoon transect and on the sea reef transect. Clearly, corals on the sea reef are not zoned in response to silt as an environmental factor, yet neither are they zoned on the lagoon reef transect where much silt is present. If weather conditions did make the water turbid on the outer reef, it would be turbid entirely across the reef, thus obliterating any expressions of growth responses to differing amounts of silt in suspension. The fact that certain silt-resistant species are found on the lagoon reefs and not on the sea reefs does not *a priori* indicate that silt is the factor responsible.

Temperature

Variations in temperature along the sea reef transect were always greatest during low tides regardless of the time of their occurrence during the daylight hours (Fig. 7), but as would be expected, the greatest variation occurred during the afternoons. In every case the inshore water in pools in quadrat 2 was one to several degrees warmer than the air temperature taken at the same place and time. Actual temperature difference ranged from 1.4° to 11.0°F. Consequently, it is primarily solar radiation, not air temperature, which warms the water during the day. Unfortunately, no early morning temperatures were taken to determine whether or not the near shore water would be cooler than the air, thus it is impossible to detect the chief factor in cooling the water, although Mayor (1918) has suggested that radiation from the surface of the water is more important than the convection of heat by the cooling air. In any event, no temperature records taken after 10 a.m. showed inshore water cooler than the air at that time.

During July and August it is evident that the ocean water 20 feet down the seaward reef slope ranges through only 0.5°F., but the range widens substantially during low tides towards the shore, reaching a maximum during our study of 12.3°F. in quadrat 2. This inshore range is only half as great as that found by Mayor at Maër Island where the surface sea water outside the reef ranged through 3.5°C. in October, indicating that the waters influenced by solar radiation on that broad reef flat affected the adjacent ocean waters far more than is true at Arno.

In addition to fluctuation in temperature across the reef flat at Arno, Wells (1951) discovered fluctuations along the reef at a particular distance paralleling the shore. Thus there are wedges of warm and cool water along the reef at low tide. The cool wedges were always found opposite re-entrant channels into which the cooler ocean water surged from outside the reef, whereas the warm wedges were always opposite the salients, characteristic of the transect area.

At high tide, regardless of the time of day, the temperature of the water over the sea reef flat is very consistent, and ranges only slightly above that of offshore waters (Fig. 8). The maximum range observed in quadrat 2 was 4°F. The rather consistent temperature from the reef margin inward to quadrat 5 is the result of strong waves of translation sweeping the cool ocean water shoreward. In quadrats 2 to 5 the warm water which was characteristic of the previous low tide still exerts a warming influence as it mixes with the sea water sweeping into it.

In the lagoon reef transect the range in temperature at low tide was approximately 5°F., far less than on the sea reef (Fig. 9). Moreover, the temperature of the shallow, rather still water in quadrat 2 was precisely the same as the air temperature of the time, 1°F. more in one instance and 1°F. less in the other.

It is clearly evident that if extremes of temperature influence the zonation of corals at Arno, they must act during periods of low water during daylight hours. Certainly the small range of variability during high tides on the sea reef would have no limiting effect on the growth or distribution of corals. On the lagoon reef there is no variation during high tides and at low tide the sharpest break in the temperature curve occurs about 250 feet from shore at the point where corals cease to flourish and only sand and reef rock occur shoreward. I do not ascribe the absence of corals shoreward from this 250-foot mark to high temperatures, but rather to the fact that only 1 or 2 inches of water cover the area inshore which would make exposure an inhibiting factor.

No particularly sharp breaks in temperature occur across the sea reef at low tide, so the gross zonal limits of kinds of corals cannot be associated directly with the presence of periods of unfavorable or favorable temperature. Instead there appears to be a limiting influence exerted by temperature, principally felt inshore, but operative probably as far seaward as quadrat 10. Certainly the wide range in temperature in quadrats 2 and 3 would be deleterious to coral growth, but we have already noted that several other factors may be just as deleterious or more so. Temperature variation, then, at low tide would seem to be a contributing factor in limiting the growth of certain corals, but it does not appear inhibiting because no sharp breaks in the zonation of corals coincide with the typical temperature curves. There is no justification for attributing zonation of corals at Arno to temperature differences as has been done by Mayor for the very broad reefs of Maër Island and of Samoa. Neither can temperature be considered one of the most important factors in zonation as was done at Bikini by Ladd, *et al.*, (1950). Rather it must be concluded that the vicissitude of temperature fluctuations shoreward makes the inshore area less favorable for coral growth than the region toward the margin where temperature conditions approach a rather steady state of little change. Evidence supporting this may be found in the distribution of such resistant forms as *Porites lutea*, which is a common inshore form but is not found near the reef margin. Experimental evidence purporting to permit the interpretation of species distribution from the degree of resistance of corals to increasing temperature is not convincing; indeed, Edmondson (1928) found that the ability of a species to endure high temperatures does not always indicate it to be a near shore form, and that resistance to temperature is not well correlated with the position of the colonies on a reef.

Salinity

Contrary to the situation at Maër Island where Mayor found virtually no dilution of waters over the reef flat either at various times of the day or states of the tide, the range of chlorinity along the sea reef transect during low tides at Arno was rather great, varying from as low as 64 per cent as concentrated as ocean water to 85 per cent (Fig. 10). A rather steady increase in chlorinity is evident from inshore waters to the reef margin where the water never varied more than 1.5 parts per thousand regardless of the tide. At no place is there a sharp discontinuity. During high tides the chlorinity was almost invariable over the entire width of the reef tract because the waves of translation reached the beach.

On the lagoon transect virtually no chlorinity gradient exists (Fig. 11). On one occasion an inshore sample was measured which was only 90 per cent as concentrated as sea water, but in all other instances no variation was noted, state of tide and time of day notwithstanding.

Because very few measurements of chlorinity gradients across reef tracts have been made, and these indicated no appreciable dilution of reef waters, and because experimental results on subjecting corals to various dilutions of sea water suggest that corals might live indefinitely and without harm if the ocean salinity were reduced to 80 per cent of normal sea water (Vaughan, 1916), the factor of dilution has been more or less dismissed as insignificant in influencing the distribution of corals except when torrential rains may coincide with low water (Mayor, 1924). The same evidence upon which the foregoing conclusions were based may be coupled with what is generally known about "critical tide factors," as discussed previously in the section on exposure, to question seriously the previous concepts of dilution as a negligible factor in the growth and distribution of corals. Such data as that presented by Mayor for corals at Maër Island where only half of the reef corals could survive 11½ hours of 50 per cent dilution and only 3 could withstand this dilution for 24 hours; and that of Vaughan (1916) and of Edmondson (1928) for Tortugas corals and Hawaiian corals respectively in which they found a dilution to 75 per cent sea water not overtly injurious, but greater dilutions injurious, over extended periods indicate that dilution does have a depressing effect, although considerable variability in resisting dilution is evident among certain corals. It follows that, coincident with periods of low water, dilution and high temperatures can act in concert to limit the growth of some corals and inhibit other less hardy forms.

Because Arno Atoll is rather typical of other atolls of the same latitudes as regards geological composition and climate, many reefs must exhibit the same variable salinity pattern as found here. In checking possible reasons for the lowered salinity across the seaward reef at low tide, rainfall and tidal status appeared to be only incidental. For example in quadrat 2, during low water on the days when the samples were collected, the chlorinity was 12.8 parts per thousand, the tide was 0.5 and 1.6 inches of rain had fallen the previous night. When the chlorinity was 17.0, the tide was 0.6 and 3 inches of rain had fallen the previous two days. During these periods of great fluctuation in chlorinity on the sea reef the chlorinity on the lagoon reef remained consistently high. The lack of fluctuation on the lagoon reef and the consistent dilution on the sea reef regardless of rainfall eliminated rainfall as a significant factor directly related to the dilution of reef waters. The only remaining source of fresh water on an atoll is ground-water. The author is indebted to Mr. Doak C. Cox, hydrologist, for clarifying the fundamentals regarding ground-water on an island such as Ine. Because this ground-water is the primary source of dilution of the reef waters, and because its principles are little known to biologists, its basic details are reviewed herewith.

Of prime importance to the accumulation and dissipation of ground-water on Arno are the geological characteristics of the atoll. Wells (1951) has described in detail the geological features of Arno which are significant in considering this subject. The islands on an atoll are mere heaps of sand and boulders on the reef platform or the top of the reef which gives shape to the atoll. Their position and the character of the materials within them are determined by shape, size and exposure of the sections of the reef on which they develop. Surmounting the beaches on the ocean sides of the island is a boulder rampart. The ocean beaches themselves contain many boulders interspersed with very little fine sand. The lagoon beaches, on the other hand, are composed primarily of sand, much of it exceedingly fine. Because the islands develop by accretions on both shores, the materials comprising the beaches on the two shores should be representative of the materials composing the islands as a whole. Thus, the permeability of the coarse ocean beach sediments should be much higher than that of the fine lagoon-beach sediments. Whether these surface conditions are typical of the underlying materials depends on whether the present environments are typical of those which prevailed while the reefs were constructed. Since we must assume that the present and past environments are similar, there is a strong possibility for the development of asymmetry in the permeability of the island.

Rain falling on the surface of an island such as Ine is in part absorbed into the ground where it percolates downward and accumulates at the surface of the salt water at sea level. The porous island rock, partly submerged in ocean water, though it does not absolutely confine the water that saturates it, provides a restriction of flow that may reduce mixing sufficiently so that if fresh water is introduced into it, an integral body of fresh water will be maintained, floating on the denser sea water in the rock and displacing it so that approximately every unit of fresh water above the ocean water level will be supported by 40 units below. This hydrostatic relationship is known as a Ghyben-Herzberg system (Wentworth, 1947; Cox, 1951).

It has been established that the amount of ground-water flowing through a sand of given cross section will be proportional to the hydraulic gradient, and that with the same hydraulic gradient in the same system but with sands of different sizes and degrees of compaction, the amount of water flowing through a given cross section will be proportional to the permeability of the sand.

On islands such as Ine the bulk of the water lost from the lens must flow to its margins at the shores, which flow can be induced only by a hydraulic gradient towards the shores. By the Ghyben-Herzberg law the higher heads inland must be balanced by greater depths of fresh water inland. If permeability were constant and the rainfall uniform all the excess rainfall must flow through the shore edges of the fresh-water body. Near shore the head is low and the thickness of fresh water small, thus this must be balanced by a high shoreward hydraulic gradient, and the rapid increase of both head and depth of fresh water inland. The fresh-water body, therefore, has a lenticular shape with a water table that is convex upward, and with a lower, salt water contact that is similar but exaggeratedly convex downward. Because sea level, which controls the position of the lens, has tides, the loss of water from the lens is controlled by a variable base, making the hydraulic gradients throughout the lens and the rate of loss variable.

Hydrologic studies have shown that Ine Island, at the site of the sea reef transect, has greater permeability on the ocean side than on the lagoon side as evidenced by the relatively low head inland from the ocean shore and the relatively high head inland from the lagoon shore (Cox, *op. cit.*). Differences in permeability were also indicated by the greater damping and lag of the tides as they move in from the lagoon shore than as they move in from the ocean shore. The water table gradients on the two sides of Ine Island indicate an effective permeability ten times, or more, greater in the zone occupied by the lens on the ocean side than on the lagoon side. A diagrammatic cross section of the Ghyben-Herzberg system at Ine Village as it is presumed to exist is shown in Figure 12.

Because the maximum head of the lens at Ine is approximately 1 foot above mean sea level, the action of the tides induces profound changes in the outflow onto the reef. The mean high tide level here is nearly three feet higher than the maximum head of the fresh water, thus the sea water effectively damps the outflow onto the reef, and, in fact, results in a reversal of slope of the hydraulic gradient. At low tide, on the other hand, lens water flows rapidly onto the reef platform and dilutes the sea water there.

If the permeability of the sediments were the same on both sides of the island the lens would be more symmetrical and the inshore waters on the lagoon reef would become diluted by the fresh-water outflow. This does not occur because of the impermeability of the fine sand characteristic of the lagoon side of the island and reef platform. The asymmetry in dilution on the two sides of the island is thus explained, and the basic principle almost certainly holds for other island areas. Variations will appear, of course, depending upon rainfall, permeability, size of island, tidal amplitude, etc.

These data indicate that lowered salinity is probably a usual occurrence during low tides across seaward reefs, and that in areas of mixed, semidiurmal tides this dilution may exist for as long as 17 to 19 hours inshore. The alteration in the metabolism of corals under these circumstances, particularly when coupled with exposure and high temperatures, certainly influences their growth unfavorably. Now and then extreme conditions occur in certain environmental factors which impart totally unfavorable situations for corals. For example, prior to the arrival of our instruments for determining chlorinity at Ine a very low, low tide was followed by a rather low, high tide, and this in turn was followed by a moderately low, low tide. During this period a torrential rain fell continuously, which, coupled with the ordinary outflow of fresh water from the lens, must have reduced the water from quadrat 6 shoreward to a salinity well below 50 per cent of normal sea water. The following morning the top three inches of the *M. gaimardi* heads had turned a light brownish color and by evening they had bleached white. That part of the colonies which had been subjected to the greatest exposure and dilution had been killed, indicating that a single day's exposure to a very unfavorable environment could be inhibiting to the hardiest of corals. It is not surprising then that the usual periods of exposure to diluted sea water during normal low tides would limit the growth of less hardy species on the shoreward portion of the reef flat.

Discussion

Of the various factors known to limit or inhibit coral growth, it appears that sharp changes or discontinuity in species distribution are influenced principally by exposure, and that critical tide factors, particularly at the level of "lowest lower high water," may be very important in the near exclusion of corals other than *M. gaimardi* from quadrats 3 to 5. The absence of any coral species on the inner, exposed slopes of the lagoon reef indicates that exposure among lagoon corals at Arno Atoll is completely inhibitive.

As important as exposure is in itself, desiccation appears to be a rather negligible factor for *M. gaimardi,* because the dense clusters of heads are invariably in shallow depressions where trapped water is available to rise by capillarity through the cavernous skeletal structure. If desiccation were the only factor involved then other spongy forms such as *Acropora* might also invade the shoreward reef flat. The differential distribution of corals inshore coupled with the development of micro-atolls implies that two or more factors are effective in regulating distribution. It has been mentioned that during periods of low water both solar insolation and dilution contribute to a widely fluctuating environment wherein only the hardiest forms find favorable existence. Seaward the environmental fluctuations are minimized until a very consistent environment is attained on the outer seaward reef slope just below the margin. The distribution of species across the reef at Ine Anchorage is an interesting one because, unlike population density which represents an absolute value and is based primarily on the amount of food available, species density is a relative value and depends mostly upon the selective action of the environment. Under optimum conditions for existence the species density should usually be very great, but it would decrease as the environmental exigencies increase. The distribution of species along the seaward reef transect at Ine bears out this hypothesis. Wide fluctuations inshore in exposure, temperature and salinity, all of which are intimately associated and mutually dependent, become progressively less variable toward the reef margin. Increase in species density appears directly correlated with a decrease in environmental variability. Except for exposure, this decrease in environmental variability is a gradual one, and the data would indicate that the effect on coral growth of such fluctuations is limiting, rather than inhibiting, and that the distribution of kinds of corals is regulated by their individual ecological valence for these variable environmental factors. The lack of variable environmental factors along the lagoon reef transect, except for exposure, results in a rather even distribution of kinds of corals so long as the water covers them at low tide. This is precisely the type of distribution one would expect.

These data indicate that on the sea and lagoon reef transects at Arno Atoll, exposure is probably the most important single factor in the distribution of kinds of coral, and is almost singly responsible for the rather sharp division between the dense inshore stand of *M. gaimardi* and the other corals seaward of it. Coincident with low water, high temperatures from solar radiation and lowered salinities from ground-water outflow mutually induce the unfavorable environment for coral growth, which becomes less limiting toward the margin of the reef. The gradual decrease in species density from the margin shoreward may be attributed to their varying tolerances to these unfavorable environmental factors. The greatest species density, found on the outer reef slope just over the margin in quadrat 11, is indicative of very favorable environmental conditions which show virtually no fluctuation daily, seasonally or annually. Silt deposition is unimportant on the sea reef, and water movement here influences primarily the form of the coral head rather than being inhibitive to particular species.

The factor of competition among corals on the sea reef transect looms up only in quadrats 6 to 9. Shoreward of quadrat 6 and in the wave impact area of the reef margin in quadrat 10, the vicissitudes of environment appear more important in the welfare of species than neighboring coral heads. In quadrats 6 and 7 *Acropora* gradually replaces *M. gaimardi* as the dominant form. Both types are corymbose and grow in thick clusters. Shoreward of quadrat 6 the environment apparently limits the vigorous growth of *Acropora* so that *Montipora* tends to crowd it out. However, if conditions are favorable for vigorous growth of *Acropora* it becomes very abundant and gives other species very little space for developing colonies. Thus, from quadrat 7 to the reef margin *Acropora* easily dominates the kinds present. Other types are located mostly in channels or depressions, and many are encrusting forms which grow in small patches on the bases of erect species. At the reef margin the heads are small and compact, leaving room for many other species capable of withstanding the impact of waves to gain a foothold.

On the lagoon transect competition between corals was accentuated even though they were not closely packed, because suitable substrate for attachment and growth was at a premium. Here erect species attached to coral boulders or dead massive heads were in severe competition with encrusting types which thickly clothed all boulders, dead columnar heads and even the bases of the live, erect types. Since virtually no adversities in environment had to be met, except for an occasional period of heavy silt suspension, the competition was mainly between coral and coral.

From the standpoint of understanding the total ecology and productivity of coral reefs, too much emphasis cannot be placed on the distribution of corals because they provide the key to the distribution and abundance of virtually every other animal and many of the plants present. Reefs in which corals rather than nullipores play the dominant role, such as those described at Arno, form communities in which the coral heads provide excellent protection and concealment for many species. The cavernous nature of the massive corals make near perfect hollows for the retreat of many fish and invertebrates, and the relatively soft consistency of the limy skeletons permits the existence of a multitude of burrowing forms. Thus, the entire assemblage of animals surrounding a coral reef will be concentrated on and in coral heads, and life abounds there in the midst of an otherwise impoverished area.

SUMMARY

1. This study was undertaken to assess more precisely the factors responsible for the horizontal zonation of corals on the sea and lagoon reefs of Arno Atoll, Marshall Islands. Only corals are used as indicator species.

2. A transect 50 feet wide was marked out across the seaward reef tract. It was marked off linearly at 50-foot intervals to form quadrats 50 feet on a side. On these transects periodic measurements were made of chlorinity and temperature. Levels of the reef flat and of the tops of coral heads were measured in relation to a datum level. Collections of corals were made in each quadrat for taxonomic determinations and the head density was estimated for the most prominent types.

3. On the transect across the sea reef tract two clearly-defined zones of coral growth are evident between the shore and the margin. *Montipora gaimardi* thickly covers the inner portion of the reef from the beginning of coral growth to a point 200 feet from shore. Seaward to the reef margin at 450 feet *Acropora* easily dominates. Just over the reef margin *Pocillopora* is most prominent on the upper 20 feet of precipitous seaward slope, and below that *A. reticulata* and *Porites lobata* become most common. The number of species of corals increases consistently seaward and the outer reef slope supports the greatest variety of kinds, although the densest population of coral heads occurs about 100 to 150 feet shoreward from the margin.

4. On the lagoon reef transect no clear-cut zonation of corals was apparent. No type comparable to *M. gaimardi* existed on the lagoon reef, and exposure evidently was completely inhibiting to all lagoon species. On the lagoonward slope *Porites andrewsi* dominated to a depth of 10–15 feet, followed by a belt of pedestal colonies of *A. reticulata*. Below this thickets of *A. formosa* were abundant and extended to the lagoon floor. Fewer species occurred on the lagoon reef than were present on the sea reef, and population density was greatest on the outer portion of the reef flat.

5. Of the various factors known to limit or inhibit coral growth, it appears that sharp changes or discontinuity in species distribution is influenced principally by exposure. The absence of any coral species on the inner, exposed slopes of the lagoon reef indicates that exposure among lagoon corals at Arno is completely inhibitive. Coincident with low water, high temperatures resulting from solar radiation and lowered salinities derived from ground-water outflow mutually induce an unfavorable environment for coral growth shoreward, but these factors become less limiting toward the margin of the reef because of their diminished variability until they gradually merge into the unvarying values characteristic of oceanic waters.

6. The gradual decrease in species density from the reef margin shoreward may be attributed to varying tolerances to unfavorable environmental factors, and the greatest species density found just over the margin was indicative of highly favorable environmental conditions.

7. Silt deposition is unimportant on the sea reef, and water movement there influences the form of the coral head rather than being inhibitive to any particular species.

8. The lack of variable environmental factors on the lagoon reef results in a rather even distribution of kinds of corals and very little or no zonation, except shoreward where exposure is inhibiting.

LITERATURE CITED

BAKER, JOHN R. 1925. A coral reef in the New Hebrides. *Proc. Zool. Soc.*, London, No. 66, pp. 1007-1019.

COX, DOAK C. 1951. The hydrology of Arno Atoll, Marshall Islands. *Atoll Res. Bull.*, No. 9, 29 pp.

DOTY, MAXWELL S. 1946. Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific Coast. *Ecology*, 27: 315-328.

DOTY, MAXWELL S. and JUSTINE G. ARCHER. 1950. An experimental test of the tide factor hypothesis. *Amer. Jour. Bot.*, 37(6): 458-464.

EDMONDSON, CHARLES H. 1928. The ecology of an Hawaiian coral reef. *B. P. Bishop Mus. Bull.*, No. 45, 64 pp.

KUENEN, PH. H. 1933. Geology of coral reefs. *Snellius Exped.*, Vol. 5, Geological results, pt. 2, pp. 1-126.

LADD, H. S., J. I. TRACEY, JR., J. W. WELLS and K. O. EMERY. 1950. Organic growth and sedimentation on an atoll. *Jour. Geol.*, 58(4): 410-425.

MANTON, S. M. 1935. Ecological surveys of coral reefs. *Gr. Barrier Reef Exped., Sci. Rep.*, 3(10): 273-312.

MAYOR, ALFRED G. 1918. Ecology of the Murray Island coral reef. *Pap. Dept. Mar. Biol., Carnegie Inst., Wash.*, 9: 1-48.

———. 1924. Structure and ecology of Samoan reefs. *Pap. Dept. Mar. Biol., Carnegie Inst., Wash.*, 19: 1-25.

TRACEY, J. I., JR., H. S. LADD and J. E. HOFFMEISTER. 1948. Reefs of Bikini, Marshall Islands. *Bull. Geol. Soc. Amer.*, 59: 861-878.

UMBGROVE, J. H. F. 1947. Coral reefs of the East Indies. *Bull. Geol. Soc. Amer.*, 58: 729-778.

VAUGHAN, T. W. 1912. The coral reefs and the life history of corals. *Carnegie Inst. Washington, Year Book* No. 11, pp. 159-162.

———. 1916. The results of investigations of the ecology of the Floridan and Bahaman shoal-water corals. *Proc. Nat. Acad. Sci.*, 2(2): 95-100.

VERWEY, J. 1931. The depth of coral reefs in relation to their oxygen consumption and the penetration of light in the water. *Treubia*, pt. II, 13: 169-198.

WELLS, JOHN W. 1951. Coral reefs of Arno Atoll, Marshall Islands. *Atoll Res. Bull.*, No. 9, 14 pp.

WENTWORTH, CHESTER K. 1947. Factors in the behavior of ground water in a Ghyben-Herzberg system. *Pacific Science*, 1(3): 172-184.

WOOD-JONES, F. 1912. *Coral and Atolls.* xxiii + 392 pp. (Lovell Reeve & Co., London).

ILLUSTRATIONS

FIG. 1.—Map of Arno Atoll showing reef types (see text for details).

FIG. 2.—Map showing the reef tracts on the seaward and lagoonward sides of Ine Island at Ine Village. The seaward reef transect is shown extending outward from Ine Village.

FIG 3.—Map showing the position of the lagoon reef transect at Makïn Islet on the southeast corner of Arno Atoll.

FIG. 4.—Variation in the number of coral species from the beach to the edge of the sea reef along the study transect at Ine Village, Arno Atoll. A profile along the transect is placed below the graph to show precise relationships between the number of coral species and varying distances from shore.

FIG. 5.—Variation in the number of coral species from the beach to the outer slope of the lagoon reef along the study transect at Makïn Islet, Arno Atoll. A profile along the transect is placed below the graph to show precise relationships between the number of coral species and varying distances from shore.

FIG. 6.—Vertical section or profile of the sea reef transect at Ine Village, Arno Atoll, showing the levels of the reef rock platform and the tops of the coral heads in relation to tidal levels. MHW denotes mean high water; MSL denotes mean sea level, etc.

FIG. 7.—Temperature variation on the seaward reef transect at Ine Village, Arno Atoll, during afternoon low tides. A profile view of the transect is placed below the graph to show relationships between temperature variation and distance from shore.

FIG. 8.—Temperature variation on the seaward reef transect at Ine Village, Arno Atoll, during afternoon high tides.

FIG. 9.—Temperature variation on the lagoon reef transect at Makïn Islet, Arno Atoll, during midday and afternoon low tides.

FIG. 10.—Chlorinity variation on the sea reef transect at Ine Village, Arno Atoll, during high and low tides. A profile view of the transect is placed below the graph to show relationships between variations in chlorinity and distance from shore.

FIG. 11.—Chlorinity variation on the lagoon reef transect at Makïn Islet, Arno Atoll, during high and low tides. A profile view of the transect is placed below the graph to show relationships between variations in chlorinity and distance from shore.

FIG. 12.—Cross section of Ine Island, Arno Atoll, showing estimated total depth and relationships of the Ghyben-Herzberg lens.

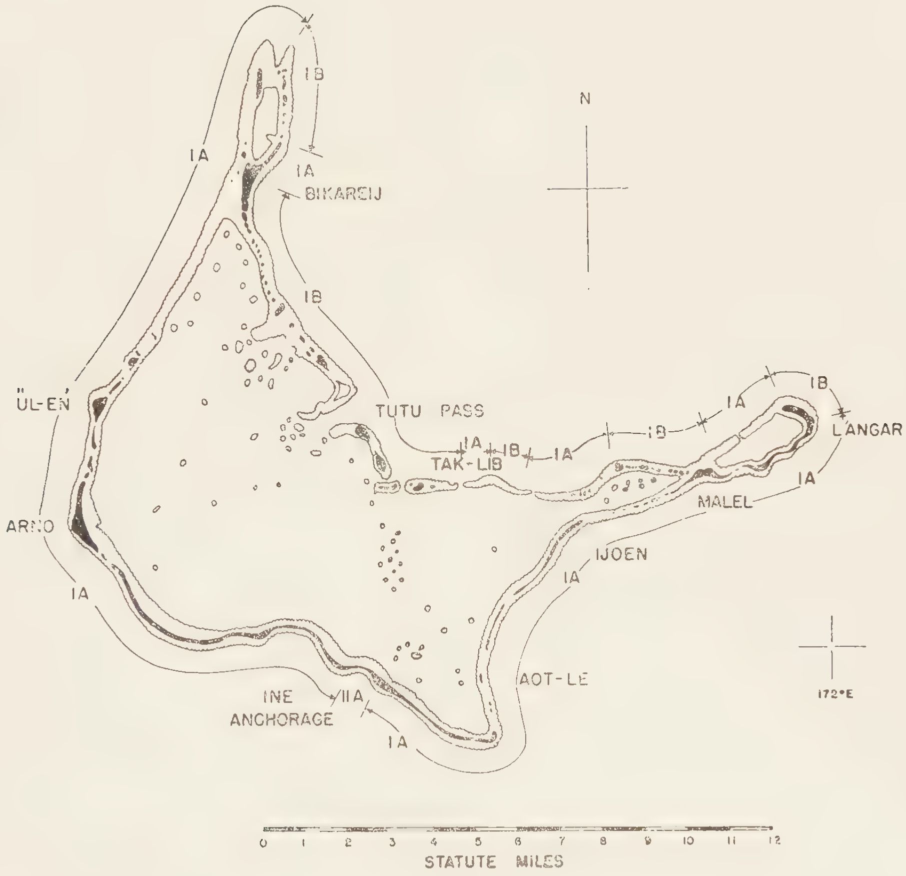

IB
N
IA
IA
BIKAREIJ
IB
ÜL-EN
TUTU PASS
IB
IA
IB
L'ANGAR
IA
IB
IA
TAK-LIB
IA
MALEL
ARNO
IJOEN
IA
IA
AOT-LE
172°E
INE
ANCHORAGE
IIA
IA
0 1 2 3 4 5 6 7 8 9 10 11 12
STATUTE MILES

FIGURE 1

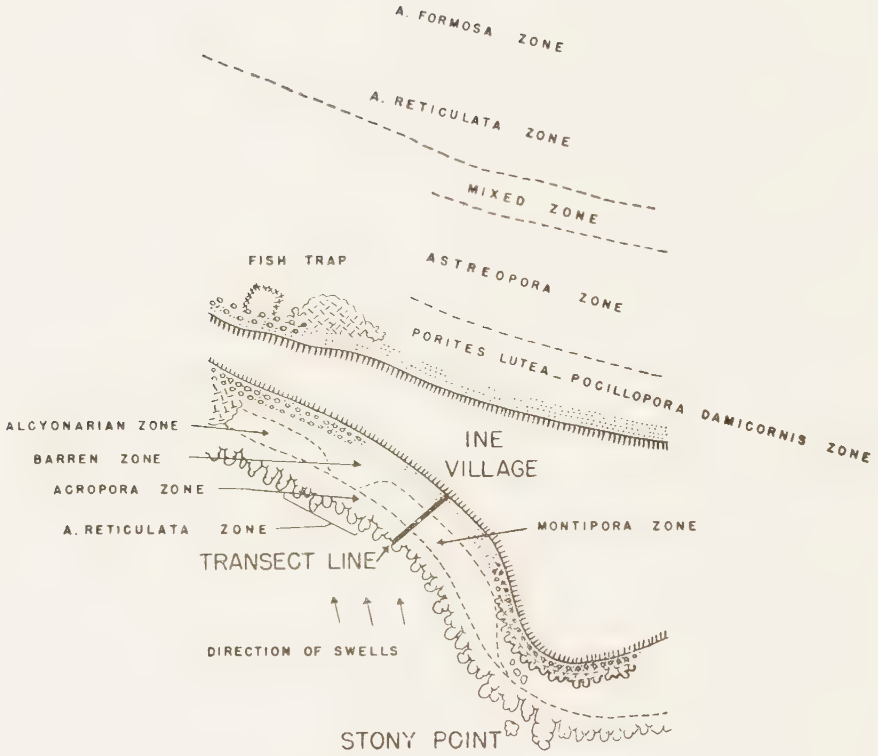

A. FORMOSA ZONE
A. RETICULATA ZONE
MIXED ZONE
FISH TRAP
ASTREOPORA ZONE
PORITES LUTEA – POCILLOPORA DAMICORNIS ZONE
ALCYONARIAN ZONE
BARREN ZONE
ACROPORA ZONE
A. RETICULATA ZONE
INE VILLAGE
MONTIPORA ZONE
TRANSECT LINE
DIRECTION OF SWELLS
STONY POINT

FIGURE 2

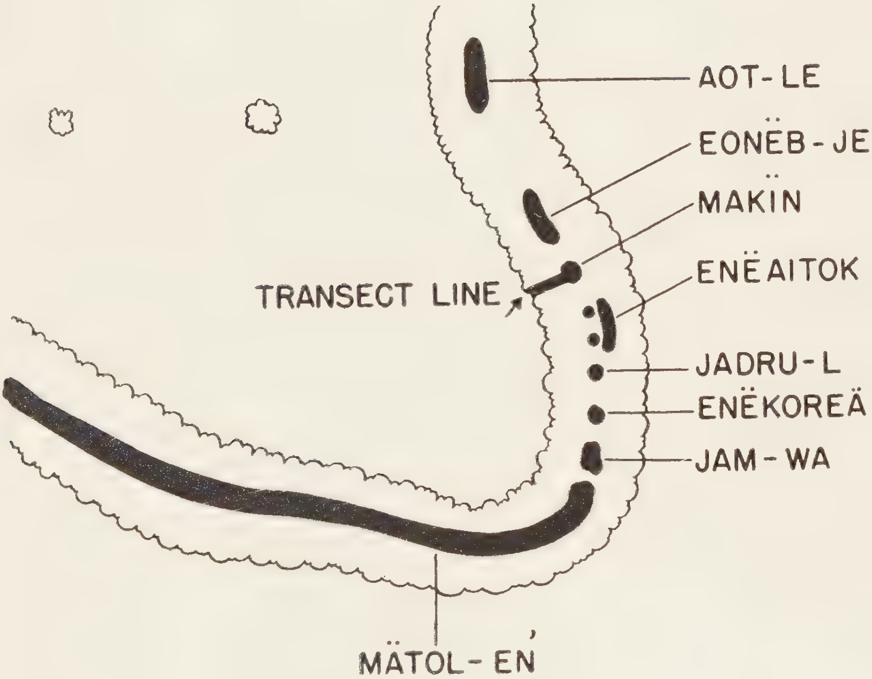

AOT-LE
EONËB-JE
MAKÏN
TRANSECT LINE
ENËAITOK
JADRU-L
ENËKOREÄ
JAM-WA
MÄTOL-EŃ

FIGURE 3

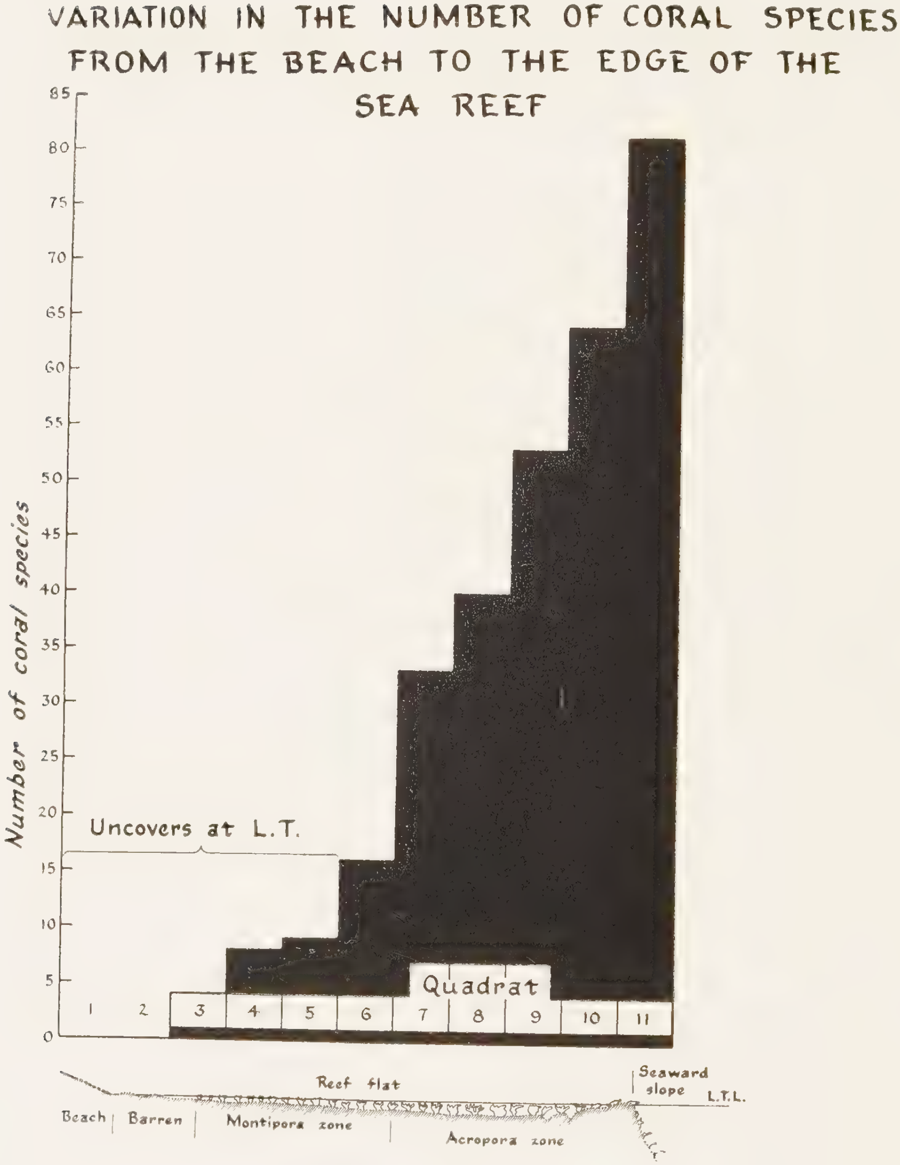

VARIATION IN THE NUMBER OF CORAL SPECIES FROM THE BEACH TO THE EDGE OF THE SEA REEF
Number of coral species
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
Uncovers at L.T.
Quadrat
1
2
3
4
5
6
7
8
9
10
11
Reef flat
Seaward slope
L.T.L.
Beach
Barren
Montipora zone
Acropora zone

FIGURE 4

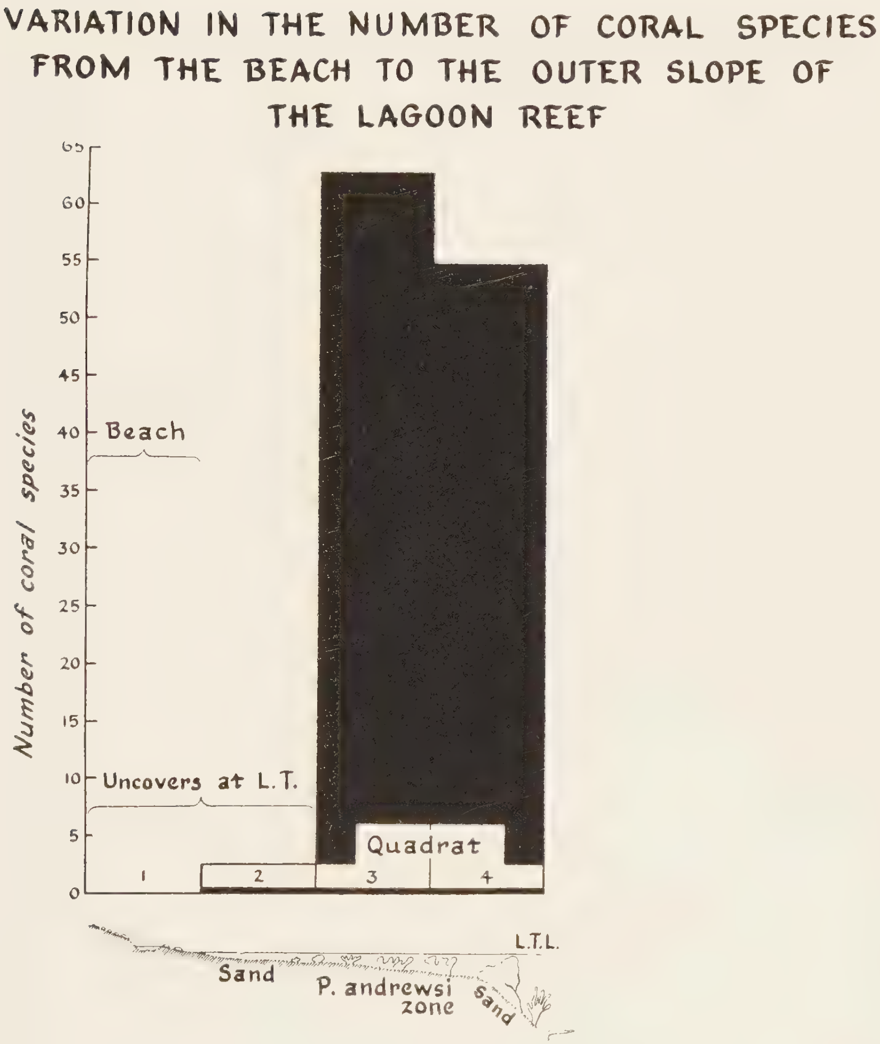

VARIATION IN THE NUMBER OF CORAL SPECIES FROM THE BEACH TO THE OUTER SLOPE OF THE LAGOON REEF

FIGURE 5

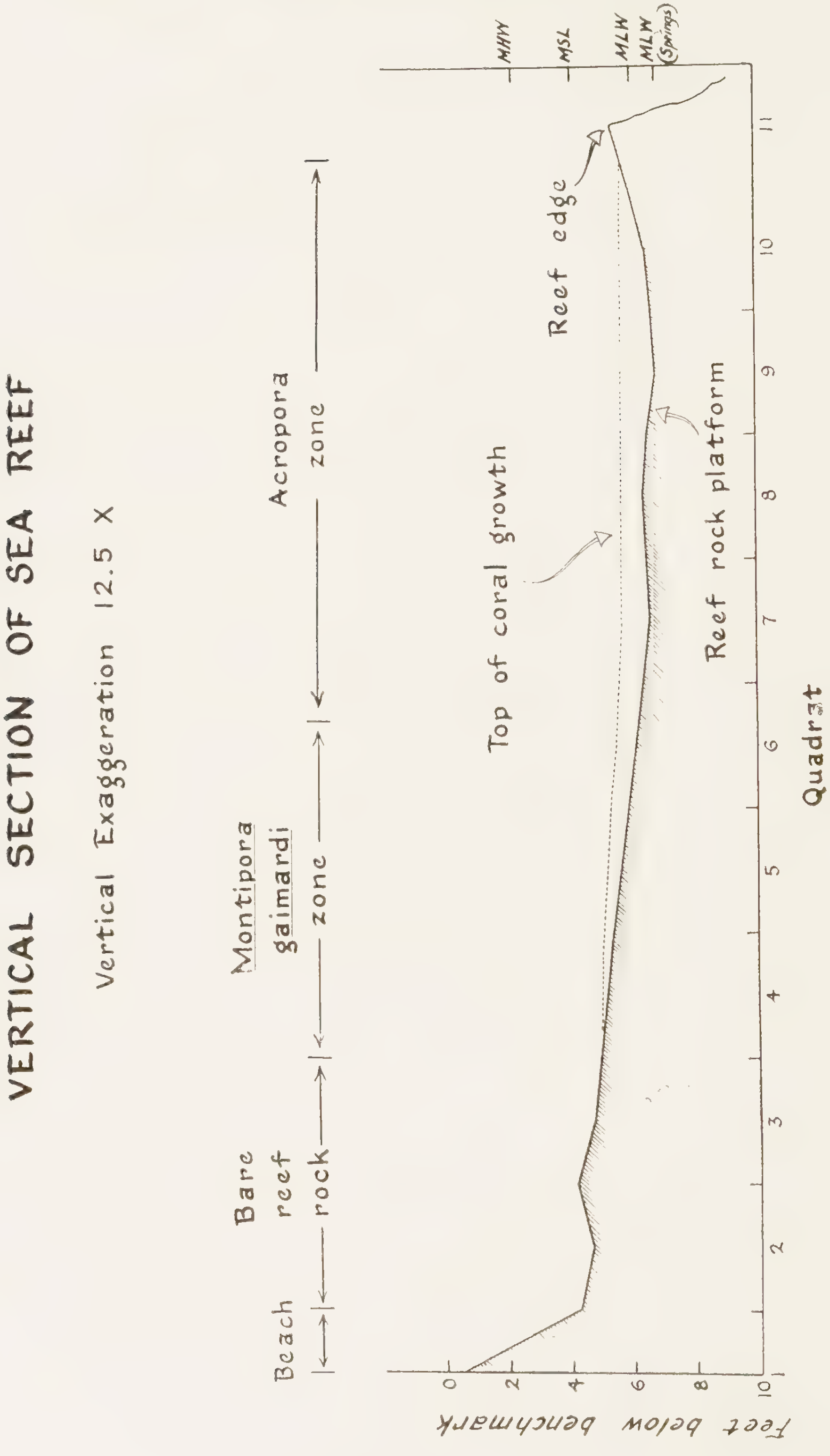

VERTICAL SECTION OF SEA REEF
Vertical Exaggeration 12.5 X
Beach
Bare reef rock
Montipora gaimardi zone
Acropora zone
MHW
MSL
MLW
MLW (Springs)
Reef edge
Top of coral growth
Reef rock platform
Feet below benchmark
0
2
4
6
8
10
Quadrat
1
2
3
4
5
6
7
8
9
10
11

FIGURE 6

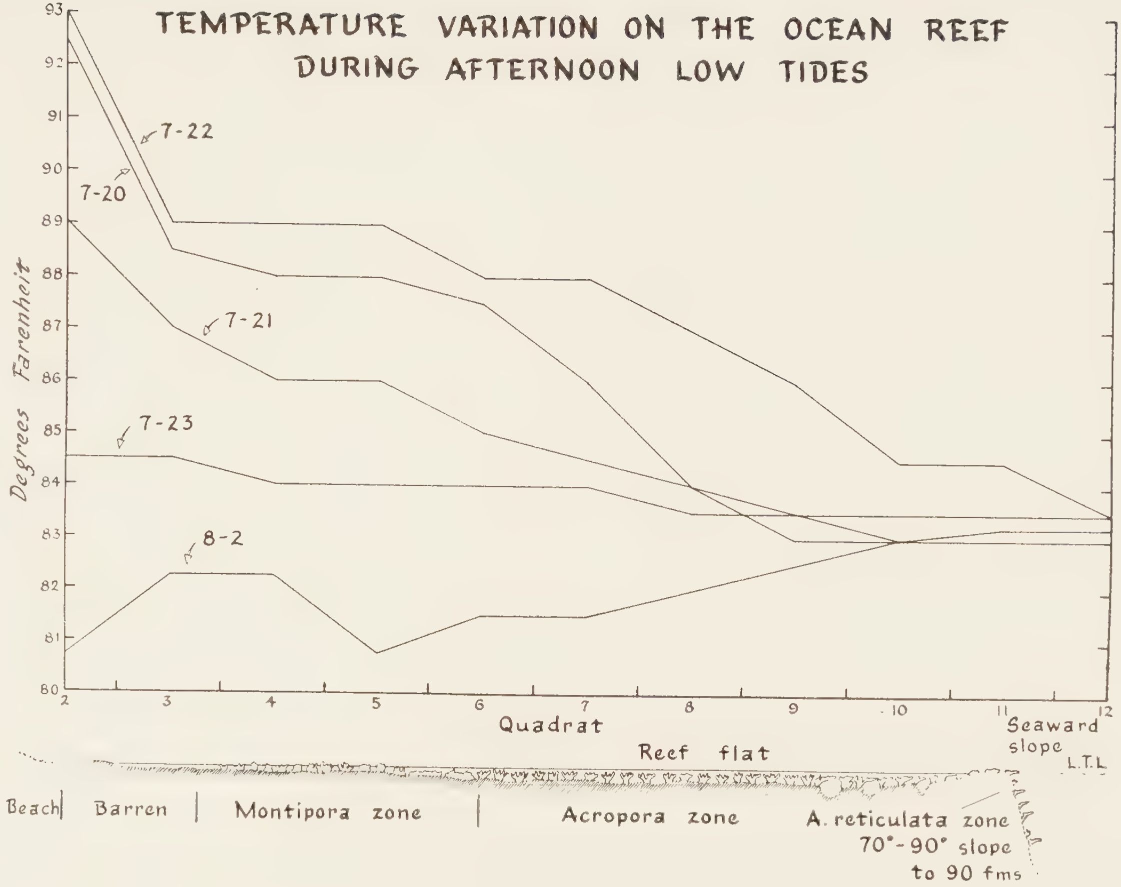
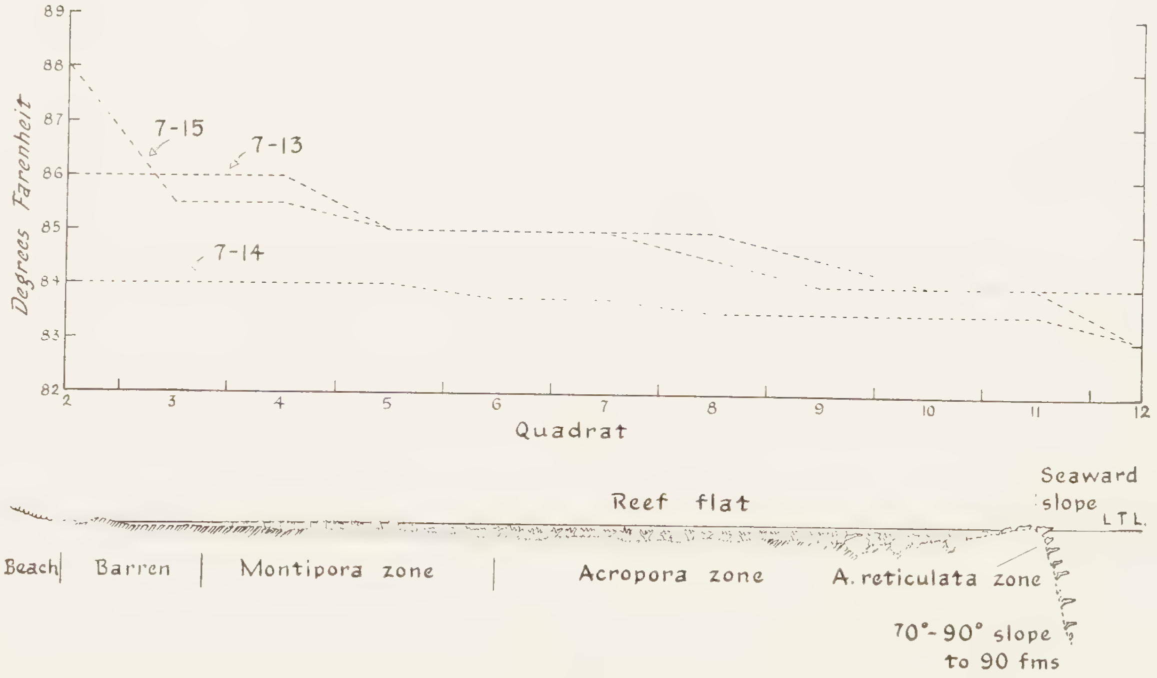

TEMPERATURE VARIATION ON THE OCEAN REEF
DURING AFTERNOON LOW TIDES
Degrees Farenheit
93
92
91
90
89
88
87
86
85
84
83
82
81
80
7-22
7-20
7-21
7-23
8-2
2
3
4
5
6
7
8
9
10
11
12
Quadrat
Reef flat
Seaward slope
L.T.L.
Beach
Barren
Montipora zone
Acropora zone
A. reticulata zone
70°-90° slope
to 90 fms

FIGURE 7



TEMPERATURE VARIATION ON THE OCEAN REEF TRANSECT
DURING AFTERNOON HIGH TIDES

FIGURE 8

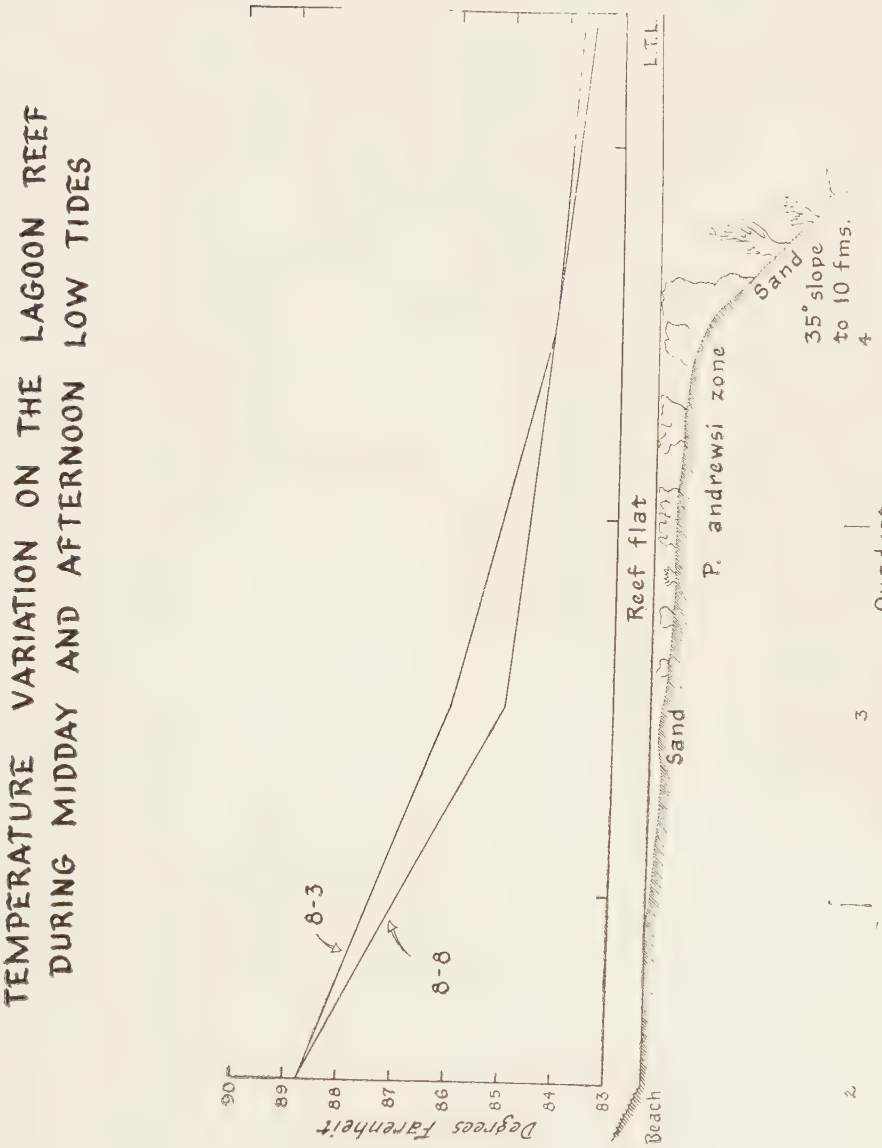

TEMPERATURE VARIATION ON THE LAGOON REEF
DURING MIDDAY AND AFTERNOON LOW TIDES
90
89
88
87
86
85
84
83
Degrees Farenheit
8-3
8-8
Reef flat
L.T.L.
Beach
Sand
P. andrewsi zone
Sand
35° slope
to 10 fms.
2
3
Quadrat
4

FIGURE 9

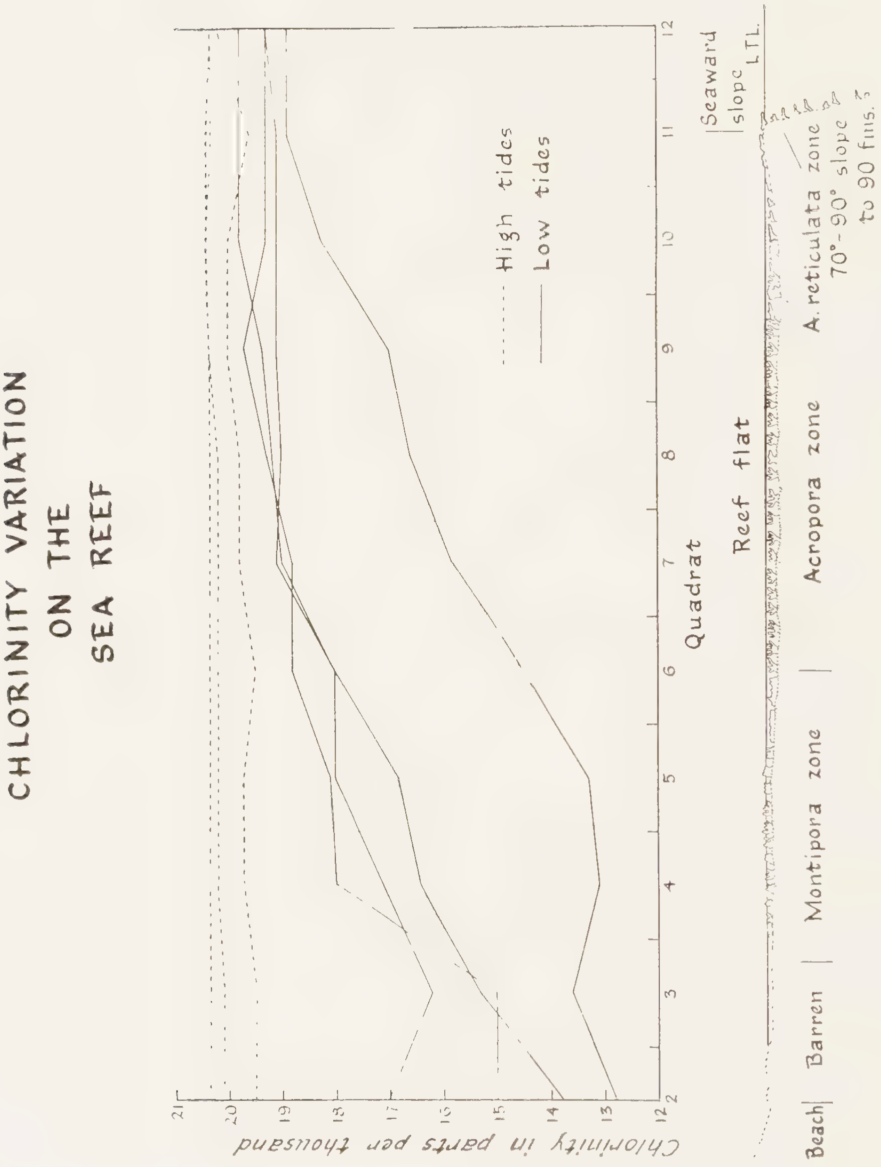

CHLORINITY VARIATION
ON THE
SEA REEF
Chlorinity in parts per thousand
21
20
19
18
17
16
15
14
13
12
2
3
4
5
6
7
8
9
10
11
12
Quadrat
High tides
Low tides
Reef flat
Seaward slope
LTL.
Beach
Barren
Montipora zone
Acropora zone
A. reticulata zone
70°-90° slope
to 90 fms.

FIGURE 10

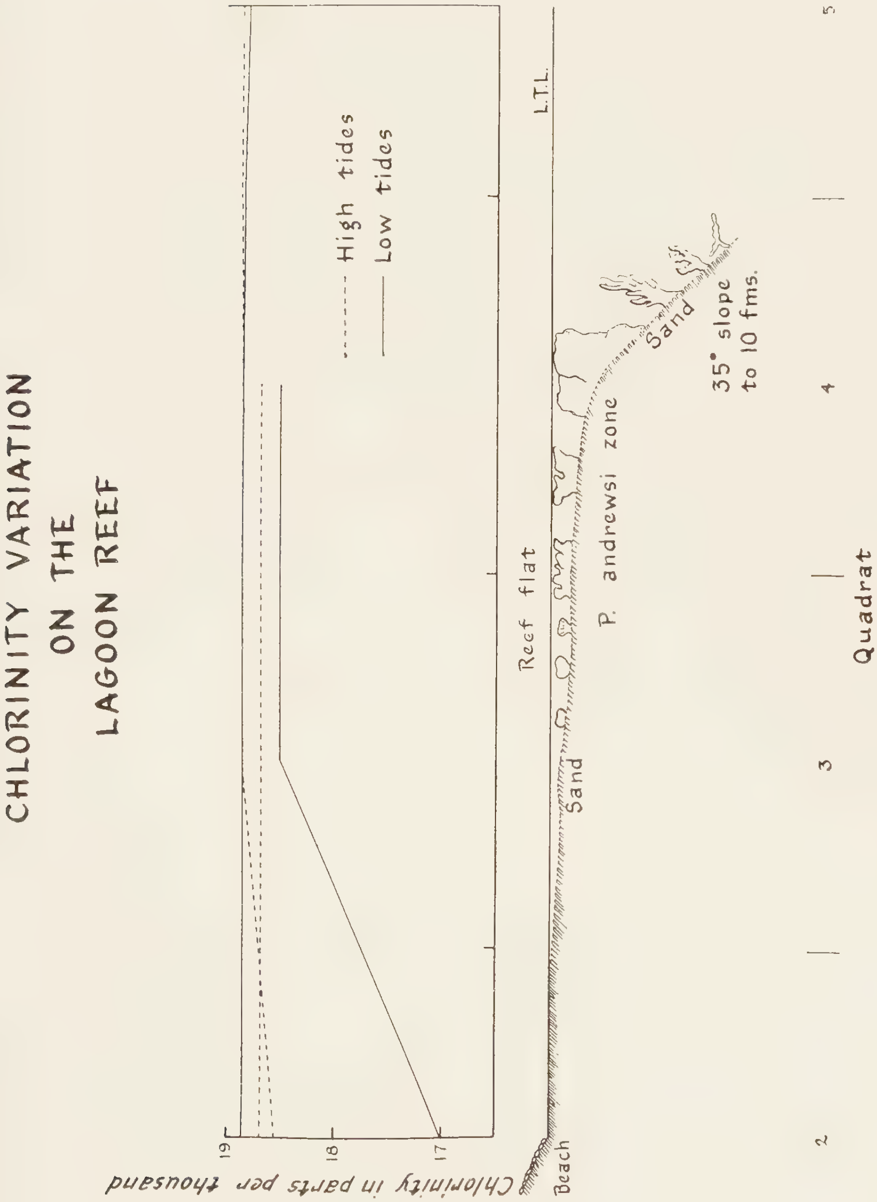
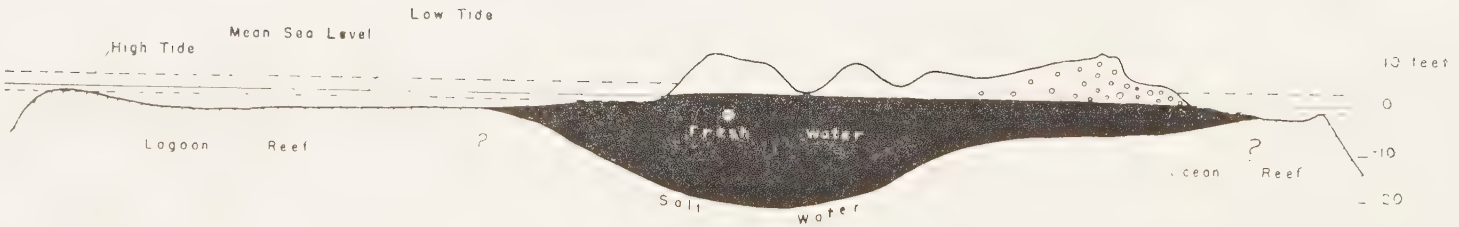

CHLORINITY VARIATION
ON THE
LAGOON REEF
Chlorinity in parts per thousand
19
18
17
High tides
Low tides
L.T.L.
Reef flat
Beach
Sand
P. andrewsi zone
Sand
35° slope
to 10 fms.
2
3
4
5
Quadrat

FIGURE 11


High Tide
Mean Sea Level
Low Tide
10 feet
0
-10
-20
Lagoon
Reef
?
Fresh water
Salt water
?
Ocean
Reef

CROSS SECTION OF INE ISLAND SHOWING TOTAL DEPTH OF GHYBEN-HERZBERG LENS. VERTICAL EXAGGERATION 10X.

FIGURE 12

SCARIDES ET MILIEU CORALLIEN: NOTES BIOGEOGRAPHIQUES

Par Théodore Monod
Muséum National d'Histoire Naturelle
57 rue Cuvier, Paris 5e, France

Les Poissons de la famille des *Scaridae* présentent, on le sait, des modifications anatomiques très profondes de la région bucco-pharyngienne, intéressant à la fois le squelette viscéral, avec sa musculature, et la base du neurocrâne, ainsi que divers secteurs de la paroi du tube digestif (sacs pharyngiens, coussinet élastique prépharyngien) . La dentition est hautement spécialisée, avec 1° un bec coupant auquel la streptognathie mandibulaire assure le jeu d'une cisaille puissante, et 2° un appareil broyeur faisant des pharyngiens transformés en véritables molaires une meule capable de moudre le calcaire corallien, l'ensemble du dispositif dès lors comparable à la dentition des Rongeurs avec: secteur antérieur incisif–diastème–secteur "jugal" molaire.

Cette morphologie paraît, à n'en pas douter, en relation avec un régime sinon exclusif du moins de prédilection. On sait en effet que si les *Scaridae* sont dans l'ensemble plus ou moins inféodés au récif corallien, c'est qu'ils se nourrissent souvent en "broutant" littéralement les madrépores dont ils sectionnent les rameaux au moyen de la pince coupante que constitue leur bec. Cette association *Scaridae*–coraux est classique (cf. par ex. S. Ekman, Tiergeographie des Meeres, 1935, p. 17).

Des observateurs ont d'ailleurs, en plongée, constaté directement les faits (Catala, Drach, etc.). D'après Drach et Guilcher (observations dans la Mer Rouge) on pourrait même, tant le "broutage" des coraux rameux est actif, attribuer dans leur destruction un rôle, peut-être non négligeable, aux Scaridés.[1]

Il ne faudrait cependant pas conclure que les Scaridés, en admettant que la famille puisse comme cela semble probable être considérée comme homogène au point de vue régime, se nourrissent exclusivement de coraux. Al-Hussaini place les "Coral-Feeders" (Scaridés et Plectognathes) dans les omnivores, nombre de petits animaux ou de fragments d'Algues se trouvant ingérés en même temps que la part de l'aliment directement empruntée au madrépore (*Publ. Mar. Biol. St. Ghardaga*, n° 5, 1947, p. 34 et sqq.)

---

[1] A. Guilcher, Formes et processus d'erosion sur les récifs coralliens du Nord du Banc Farsan (Mer Rouge), (*Rev. Géomorphol.* Dyn., II, no. 6, 1952, pp. 261-274, 5 figs.):

"Un autre fait assez curieux a été observé par le Commandant Cousteau et le Docteur Nivelleau au cours d'une plongée a Shab Suleim. Ils ont vu de grands poissons arracher des morceaux de corail vivant qu'ils mangeaient; les déjections de ces poissons, observées par les memes plongeurs, consistaient en sable. Il faut donc admettre que ces poissons sont un agent de production de sable a partir du corail, autrement dit un agent d'erosion. Le sable qui forme une pellicule sur les petits replats externes est en partie leur oeuvre." (pp. 271-272).

Le même auteur avait signalé auparavant (*Bull. Inst. Egypte*, 27, 1945, p. 350) que *Pseudoscarus sordidus* (Forssk.) ingérait en même temps que des fragments de madrépores del Algues et pouvait prospérer, en aquarium, même en l'absence de tous coraux: "the fish feeds on the algal masses growing on stones in the aquarium." On doit donc regarder ce Scare comme omnivore "feeding on coral flesh and marine plants. The fish obtains this food by scraping the surface of stony coral, grinds it and digests whatever organic material contained in it."

Sagemehl (*Morph. Jahrb.*, X, 1885, p. 201) signalé dans les sacs pharyngiens de divers Scares surtout des Algues, mais ëgalement des Hydraires, des fragments d'Eponges, du calcaire corallien.

Ce dernier ne constitue donc point, même en milieu récifal, l'unique matériel ingéré et il va sans dire d'ailleurs qu'il n'est accepté qu'à titre de support de l'aliment organique recherché (appartenant ou non au Madrépore ou au Millépore, et pouvant comprendre, outre des Algues, des éléments de la faune associée aux coraux et habitant leurs anfractuosités, Crustacés, Vers, Mollusques, etc).

Il est intéressant d'examiner le régime des Scares dans une région sans formations madréporiques, au Sénégal par exemple. Voici à cet égard quelques indications, portant sur des spécimens pêchés à Gorée, près de Dakar.

Sparisoma cretense

N° 1 – Bouillie verte, Algues (Corallines, Diatomées), débris de Balanes – Sacs pharyngiens: Algues, Crabes, Balanes.
N° 2 – Bouillie verte, Algues vertes, Corallines, Balanes, Gastéropodes.
N° 3 – Algues, Corallines, Balanes.
N° 4 – Algues.
N° 5 – Bouillie verdâtre, quelques Diatomées.
N° 20 – Bouillie verte, Algues, fragments de Balanes et de Mollusques, radioles d'Oursins, sable gris.
N° 22 – Bouillie sableuse verte, Algues, fragments de Balanes, Mollusques (1 Marginelle, 2 extrémités de *Bittium*), 1 débris de Crustacé Décapode, 1 débris de bras d'Ophiure, fragment de radioles d'Oursins.

Pseudoscarus hoefleri

N° 8 – Bouillie grise, Balanes.
N° 23 – Bouillie de Balanes broyés.

J. Cadenat me signale qu'à Gorée les *Sparisoma* et *Pseudoscarus* se prennent à la ligne amorcée de Crabes (*Xantho Leptodius inaegualis*).

En somme, pour les Scares sénégalais, un régime durivore, mais admettant une certaine proportion de matière végétale, dont nous ignorons d'ailleurs dans quelle mesure elle est spécifiquement recherchée ou avalée en même temps que d'autres proies, les Balanes par exemple.

Dans l'état, très imparfait, de nos connaissances, on peut donc admettre d'une part que, dans l'ensemble, les Scaridés sont bien un groupe écologiquement lié au milieu corallien, d'autre part que si des adaptations morphologiques très poussées rendent les Scares capables d'aller jusqu'au sectionnement et au broyage du calcaire corallien, ils se contentent souvent d'un moindre degré de sclérophagie.[2]

La liaison Scaridés — milieu récifal paraît, historiquement, primitive. En effet, les Pharyngognathes, Scaridés, Labridés, Phyllodontidés, apparaissent à l'Eocène. Le *Scarus tetrodon* Pomel provient de l'Yprésien de l'Oise. Au Miocène, les Scaridés sont connus d'Europe, d'Asie et de Californie.

Il semble difficile de ne point penser que dès leur apparition les Scaridés se sont trouvés associés au milieu récifal dont une transgression téthysienne chaude facilitait, à l'Eocène, comme elle l'avait fait auparavant et comme elle devait le refaire par la suite, l'extension vers le Nord.

La limite septentrionale des récifs coralliens avait en effet, aux époques favorables, atteint des latitudes relativement hautes[3]: 60° au Trias, 58° au Jurassique, 47° au Crétacé inférieur, 50° au Crétacé supérieur; ils n'atteindront plus que 35° au Pliocène, à peine 30° aujourd'hui.

Au début du Tertiaire la faune corallienne prend peu à peu son aspect actuel et continue à prospérer dans les eaux téthysiennes avec cependant déjà quelques différenciations "transversales" entre la partie orientale et la partie occidentale de la Théthys.

A partir du moment où le domaine oriental est définitivement séparé, dans l'hémisphère nord, du domaine atlanto-méditerranéen, au Mio-pliocène, les contingents coralliens atlantiques vont se trouver non seulement coupés de l'énorme masse corallienne demeurée indo-pacifique, mais exposés à des variations du milieu physique qui leur seront, parfois, funestes au point d'entraîner localement leur complète disparition.

Si les *Scaridae* sont bien, comme on doit le penser, tributaires, pour une large part, du récif, on doit s'attendre aussi à découvrir quelque relation actuelle entre leur distribution et celle des formations madrébrand 1928)

---

[2] "Durophagie" souvent employé est incorrect, étant hybride: un éventuel "durivore" ne pouvant guere donner du substantif, on peut accepter "sclérophage, sclérophagie."

[3] G. Ranson, Géonémie, écologie et répartition géographique des coraux constructeurs de récifs. Coraux et climats. *C. R. Som. Séances Soc. Biogéogr.*, no. 233-35, 1950, p. 77-88.

A défaut d'un calcul, dont les éléments nous manquent, portant sur des nombres d'individus, ou mieux des poids, rapportés à quelque unité de surface ou de volume, nous force de chercher une autre facon d'exprimer le développement local de la famille. A titre d'indication sommaire, le nombre d'espèces par région peut servir.

Il donnerait, approximativement:

A. Indo-Pacifique

1. Côte occidentale de l'Amérique (Panama) : 20 (Meek et Hildebrand 1928)
2. Polynésie: 60 (Fowler 1928)
3. Samoa: 90 (Jordan et Scale 1906)[4]
4. Japon: 3 (Jordan, Tanaka et Snyder 1913)
5. Indonésie: 49 (Weber et Beaufort 1940)
6. Philippines: 44 (Roxas et Martin 1937)
7. Hawaï: 27 (Jordan 1925)
8. Australie (Queensland) : 15 (McCulloch et Whitley 1925)
9. Australie (Sud) : 9 (Waite 1921)
10. Indes: 12 (Day 1878-88)
11. Mer Rouge: 12 (Klunzinger 1871)
12. Madagascar région: 44 (Sauvage 1891)
13. Afrique du Sud: 7 (Smith 1949)

B. Atlantique — Méditerranée

14. Sénégal: 4 (Cadenat)
15. Méditerranée: 1 (*Sparisoma cretense*)
16. Brésil: 16 (Fowler 1942)
17. Curacao: 19 (Metzelaar 1939)
18. Bermudes: 16 (Bean 1906)
19. Cuba: 14 (Jordan et Swain 1884–85)
20. Haïti: 15 (Beebe et Tee Van 1928)
21. Porto-Rico: 15 (Evermann et Marsh 1900)
22. Antilles et Golfe du Mexique: 40 (Jordan et Evermann 1898)

Il est donc évident qu'il existe une correspondance certaine entre la richesse d'une région en Scaridés, quant au nombre des espèces et sans doute aussi des individus, et le degré de son développement corallien. Le Scaridé est indubitablement inféodé au récif et il est probable que, né au contact des récifs paléogènes, il aura biologiquement et géographiquement suivi le sort de ces derniers: disparition à peu près totale dans la zone centrale de l'ancienne Téthys, survivance et prospérité dans les deux secteurs où s'est réfugié le faciès récifal: Antilles vers l'Ouest, Indo-Pacifique vers l'Est.

---

[4] Et non 250 (Sven Ekman, Tiergeographie des Meeres, 1935, p. 17), chiffre corrigé dans la seconde édition, Zoogeography of the Sea, 1952, p. 19.

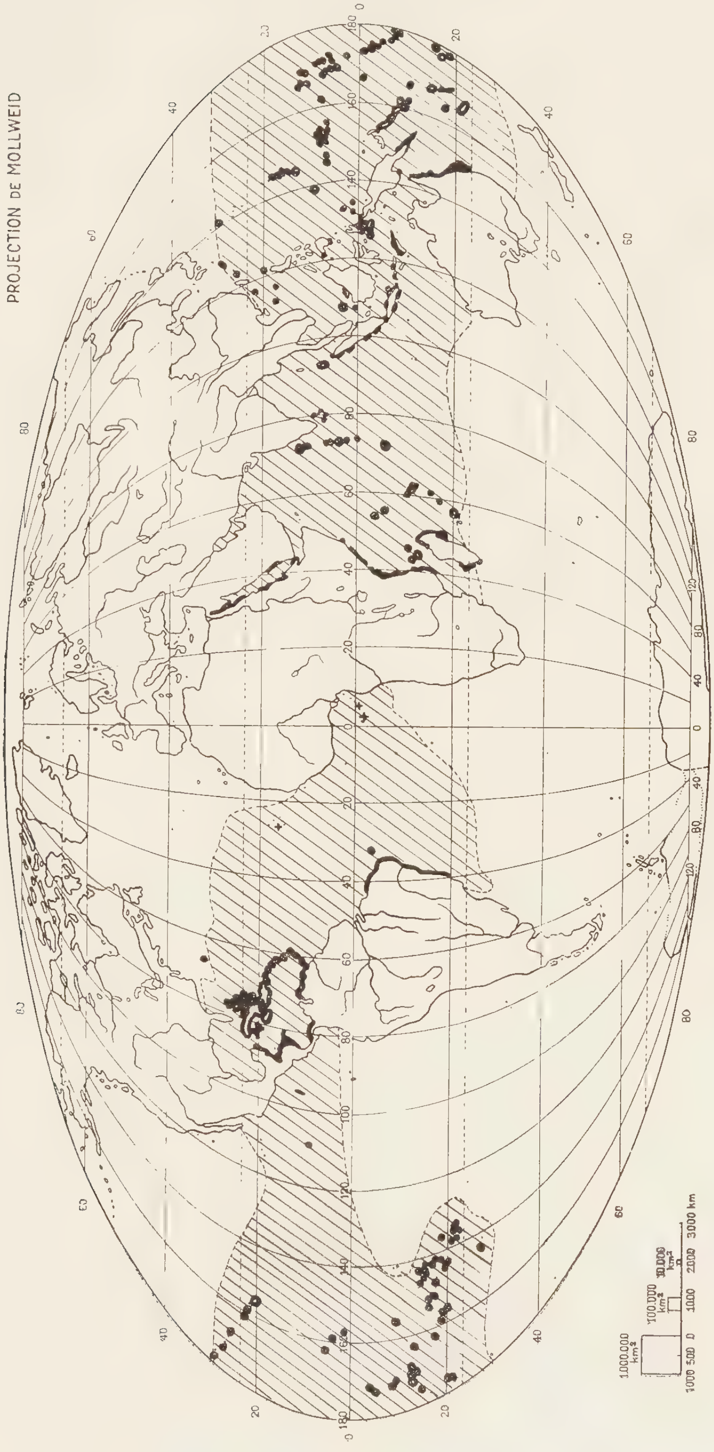
On peut donc, semble-t-il, considérer l'unique Scare de la Méditerranée et les quelques espèces ouest-africaines comme des éléments de caractère relicte, témoins demeurés sur place d'une époque antérieure.

Il n'est même pas interdit de supposer que principalement brouteurs de Coraux à l'origine, c'est secondairement que ces types privés par la péjoration du milieu de leur biotope originel, se seront adaptés à des types nouveaux et atténués de sclérophagie qui, primitifs, n'eussent sans doute pas justifié un appareil sécateur et broyeur aussi puissant puisqu'il est pratiqué par des formes beaucoup moins armées (p. ex. Labridés).

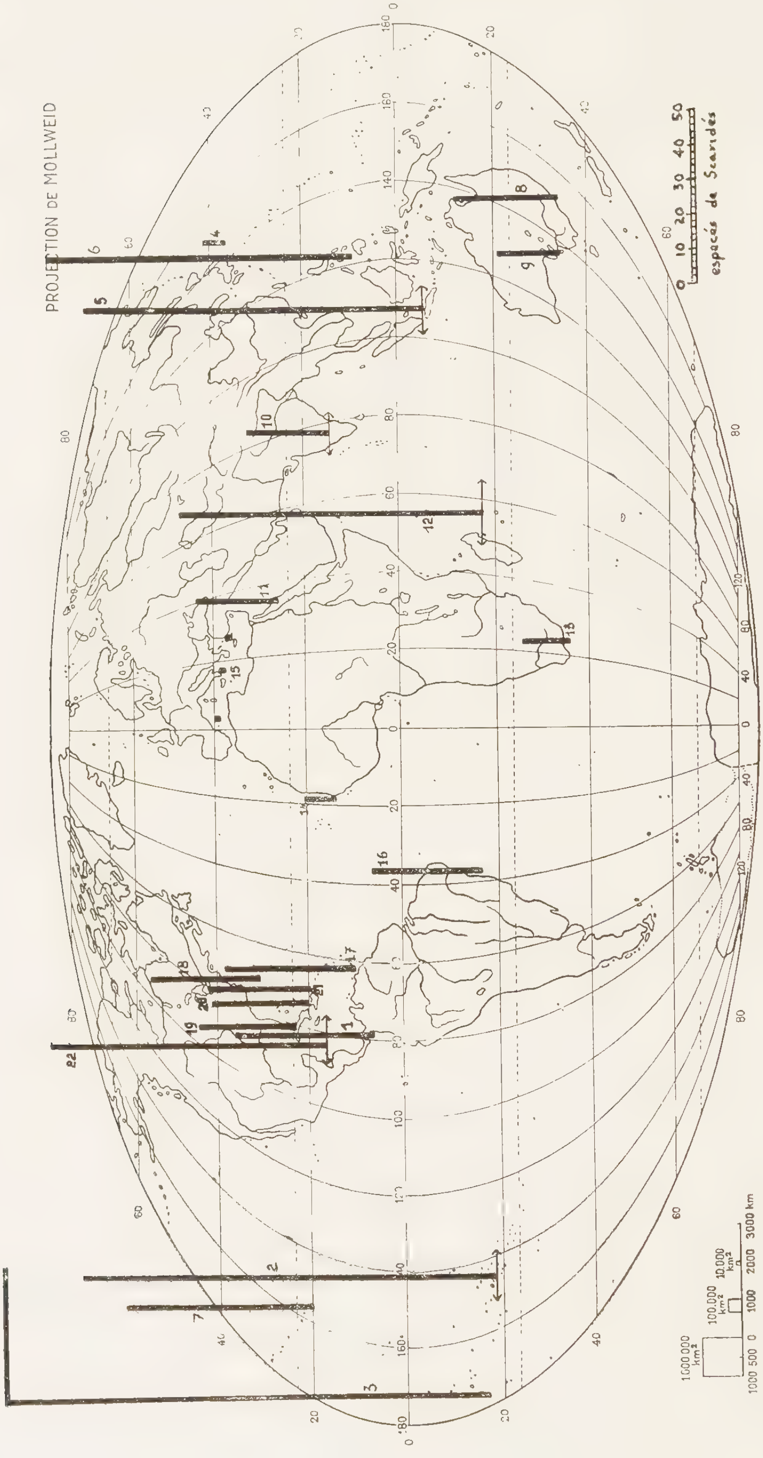
LEGENDE

Carte 1.—Zone "potentielle" de croissance des récifs coralliens; principales régions récifales en noir. Sources: Atlantique (d'après G. Schott, Geschichte des Atlantischen Ozeans, 3. Aufl., 1942, pl. XXIV), Indo-Pacifique (d'après G. Schott, Geschichte des Indischen und Stillen Ozeans, 1935, pl. III). La répartition paraît, pour l'Atlantique, forte par rapport à la carte de Joleaud, Atlas de Paléobiogéographie, 1939, pl. VII et, pour l'Indo-Pacifique, un peu schématisé par Joleaud, *loc. cit.*, mais relativement modeste par rapport à d'autres essais (p. ex. W. Schott, d'après Joubin, 1912, *in* G. Schott, *loc. cit.*, pl. V). Les croix nous indiquent des formations coralliennes n'atteignant pas, ou à peine, le stade récifal. La limite nord indiquée est l'isotherme de 20° en février, la limite Sud, l'isotherme de 20° en août, sauf dans le Pacifique oriental où elle suit sensiblement l'isanomale O de février (d'après G. Schott, *loc. cit.*, pl. XXV), tracé qui explique l'absence de récifs aux Marquises et plus à l'Ouest encore.

Carte 2.—Nombre d'espèces de Scaridés pour un certain nombre de régions (voir le exte).


PROJECTION DE MOLLWEID
1.000.000 km²
100.000 km²
10.000 km²
1000 500 0 1000 2000 3000 km

CARTE 1


PROJECTION DE MOLLWEID
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
0 10 20 30 40 50
espacés de Scaridés
1000 000 km²
100 000 km²
10 000 km²
1000 500 0 1000 2000 3000 km

CARTE 2

OBSERVATIONS SUR LES FACTEURS BIOLOGIQUES DE LA DISSOLUTION DU CALCAIRE D'ORIGINE RECIFALE DANS LES TUAMOTU

Par Gilbert Ranson
Muséum National d'Histoire Naturelle de Paris, France

Résumé

Dans cette Note il est démontré que les Algues lithothamniées ainsi qu'une Cyanophycée, *Entophysalis granulosa,* de la zone noire des embruns, sont des "rongeuses" de calcaire dont l'oeuvre est considérable dans le monde entier. Leur activite s'ajoutant à celle des Algues perforantes proprement dites et de certains animaux perforants, est l'élément fondamental de la dissolution du calcaire côtier.

L'activité particulière de l'*Entophysalis* démontre que la dissolution du calcaire aussi bien aérienne que sous-marine ou encore endolithique qu'épilithique, n'est pas le fait de la variation du ph de l'eau, la nuit, par suite de l'excrétion de CO_2 par les Algues. Elle ne peut qu'être liée à la sécrétion par l'Algue, d'un acide organique dont le sel de calcium est soluble dans l'eau.

L'*Entophysalis* n'est pas l'agent de formation du beachrock. Au contraire, elle le détruit.

Il est montré que le creusement du plateau côtier, sous le niveau des bas d'eau (et peut être la forme déchiquetée de la bordure sous-marine du plateau côtier; ceci à titre d'hypothèse seulement), la sculpture en cupules ou cuvettes du plateau côtier, aussi bien que de tous les éléments de la zone des embruns, sont le résultat de la croissance et de l'activite particulière de ces Algues.

Dans une autre note j'ai dit que les Iles des Tuamotu ne sont ni des récifs, ni des atolls actuels. Ce sont des socles de calcaire corallien fossile (anciens atolls soulevés), sur les pentes sous-marines desquels se développent de nouveaux récifs frangeants, vivants, actuels; ces derniers sont les seules formations auquelles on puisse accorder le nom de récifs; tout le reste est du calcaire corallien fossile. Il est par conséquent absolument erroné de désigner sous le nom de "pente du récif", de "plateau récifal" (souvent appelé "récif frangeant"), et de "récif" les divers éléments de ces Iles. Il ne s'agit en fait, respectivement, que de la pente du socle de l'Ile, du plateau côtier d'abrasion et du socle de calcaire corallien fossile dont est constituée l'Ile.

L'état actuel des Iles, constituées, pour la plupart, par une succession d'îlots plus ou moins isolés les uns des autres, est le résultat de l'abrasion au niveau de la mer. Les zones de sédiments consolidés ont été totalement détruites. Il en subsiste un plateau côtier légèrement au-dessous du niveau du bas d'eau. La mer passe par dessus, et communique par là avec le lagon. Les blocs coralliens consolidés des récifs proprement dits, ne sont détruits que plus lentement. Ce sont les îlots boisés avec des plateaux côtiers de largeur variable.

Examinons plus attentivement ce plateau côtier pour comprendre comment se fait l'abrasion. Sa bordure extérieure, où battent les vagues, est couverte par l'épaisse digue ou trottoir à Lithothamniées. Ces Algues calcaires ne prennent un développement important qu'en cet endroit précis: l'angle de la pente et du plateau, sur 4 ou 5 mètres sous l'eau et 4 ou 5 mètres vers la plage. Au large on sait qu'elles peuvent vivre très profondément, 100 mètres et plus. Mais elles n'y sont plus que sous forme d'une légère pellicule. J'ai fait récolter, par 6 mètres de fond des *Acropora* dont le pied en était fortement incrusté.

Si nous nous dirigeons du bord du plateau vers la plage, nous constatons que ces Algues calcaires recouvrent toute la surface du plateau côtier, d'une couche de plus en plus mince, partout où de l'eau subsiste à marée basse, ce qui se rencontre parfois jusqu'au pied de la falaise, au niveau des ilôts.

Ce plateau côtier présente le plus souvent une surface extraordinairement irrégulière: cuvettes plus ou moins profondes et pointes rocheuses aigües proéminentes. Dans toutes les cuvettes on constate une grande activité des Lithothamniées; elles les remplissent parfois totalement et tout s'effondre lorsqu'on y pose le pied. On trouve des cuvettes de toutes dimensions. Depuis les toutes petites cupules où l'on voit les Lithothamniées naissantes, avec de petits mamelons blancs reproducteurs, donnant l'impression que le sol semble couvert "d'ulcères" qui rongent la pierre, jusqu'aux larges cuvettes aux bordures abruptes encroûtées de grosses masses mamelonnées d'Algues calcaires, il y a tous les intermédiaires. Une longue observation de ces faits m'ont amené à penser que ces cupules et ces cuvettes étaient l'oeuvre des Lithothamniées. D'autres faits m'ont permis, par la suite, de comprendre que hors l'action des Oursins, toutes les sculptures en cupules, dans les calcaires côtiers, sont l'oeuvre d'Algues.

Soupconnant l'action dissolvante du calcaire par les Algues lithothamniées j'ai examiné l'action de l'une de ces Algues calcaires encroûtantes sur les Coraux. Partout j'ai observé à la loupe binoculaire l'effet de destruction progressive des éléments coralliens encroûtés. Un petit bloc d'Astreide m'a paru en être la plus belle démonstration. Il se présente comme un pseudo-atoll avec une couronne de calices, (vivants au moment de la récolte), et une dépression au centre. Cette dernière est tapissée d'une couche appréciable de *Porolithon onkodes* (Heyd.), Fosl.[1], épaissi par endroits, en mamelons. Cette Lithothamniée renferme de nombreux tubes de *Vermetus.* L'Algue calcaire ne se fixe jamais sur du corail vivant. Mais si elle trouve un support: calice mort par suite d'ensablement ou tube de Vermet ayant émergé en perforant le corail entre deux calices, l'Algue s'installe puis s'étale. Comme on peut le voir sur les bords internes de la couronne, le fauillet marginal de l'Algue recouvre progressivement les calices vivants, les "étouffe". Lorsque ces derniers sont débarrassés de leur substance vivante, l'Algae "ronge" par dissolution progressive, les calices jusqu'à leur disparition totale. On peut voir tout le tour du bord interne de la couronne de l'échantillon en question de nombreux calices présentant tous les stades d'attaque et de dissolution totale des calices du corail. A la loupe binoculaire on remarque, en certains endroits, le début de cette attaque, par dissolution des aspérités des septes, puis des septes eux-mêmes. Toute la cavité centrale de cet échantillon est l'oeuvre du *Porolithon onkodes.* Si nous connaissions la date du début de l'attaque, nous pourrions fixer la vitesse de dissolution du calcaire par l'Algue. Cette activité de l'Algue en question est absolument évidente. Madame Weber van Bosse[2], l'avait soupconnée.

Certaines Algues lithothamniées sont sans aucun doute possible, des "rongeurs" de calcaire. Le creusement du plateau côtier, au-dessous du niveau du bas d'eau, est en majeure partie leur oeuvre qui est gigantesque.

La profondeur relativement uniforme (plus grande dans les zones totalement abrasées de sédiments consolidés que dans la zone des îlots), à marée basse, du plateau côtier est certainement une résultante de leur biologie.[3]

Les Oursins, par endroits, creusent aussi des cupules dans la dalle calcaire, mais leur activité est très localisée et dans l'ensemble très faible à côté de celle de ces Algues calcaires.

Sur les côtes Est, Sud-Est et Sud de Hikueru (côtes les plus exposées au vent), c'est le *Porolithon craspedium* Fosl.[4], rougue saumon subbranchu qui domine. Sur les côtes Ouest, Nord-Ouest et Nord, c'est le *Porolithon onkodes* (Heyd.) Fosl. encroûtant.

* * *

Si le pied de la falaise est à sec, pendant le bas d'eau, et à cette condition seulement, la roche y est abondamment perforée par des animaux variés dont les plus actifs et dont l'oeuvre est la plus spectaculaire sont, à Hikueru: *Lithotrya nicobarica* Reinhardt[5] et *Physcosoma* (= *Phascolosoma*) sp. nov.[6]

---

[1] Détermination de Mde. Paul Lemoine.

[2] Dr. A. Weber van Bosse (Eerbeek), *Mém. Mus. Roy. Hist. Nat. Bruxelles*, Vol. VI, fasc. 1, 1932.

[3] Il est bien possible, mais ceci a titre d'hypothese, que la sculpture du bord du plateau cotier, soit l'oeuvre de l'activité des lithothamniées,

[4] Détermination de Mde. P. Lemoine.

La pierre, sous leur action, devient comme du bois perforé par les tarets. Le terme de "pierre pourrie", lui convient parfaitement. La vague a peu d'effort à accomplir pour en briser des morceaux. C'est ainsi que la falaise recule. Non seulement ils dissolvent le calcaire des galeries où ils logent, mais l'entrée extérieure de leur canal est en forme d'entonnoir plus ou moins large. Il faut encore mentionner, tout spécialement les Eponges du genre *Cliona* dont l'activité est très grande dans les Tuamotu. L'oeuvre de l'ensemble de ces organismes est très importante dans la dissolution et l'abrasion. La question est bien connue depuis S. Gardiner[7], Mayor[8] et G. W. Otter[9] entre autres.

* * *

Tous les échantillons d'aspérités du plateau, détachées des environs du pied de la falaise, présentent, s'ils sont examinés à la loupe binoculaire, une couche superficielle d'un blanc laiteux contrastant avec l'intérieur. Elle est cariée et se désagrège facilement sous l'action de la pointe sèche. On y voit d'innombrables petits filaments bleus d'une Algue perforante Cyanophycée. Je ne peux pas dire quelle est sa distribution exacte sur le plateau.

Le rôle des Algues perforantes dans la dissolution du calcaire (aussi bien marin, d'eau douce que terrestre) a depuis longtemps été souligné. (Gardiner[10], Bornet et Flahaut[11], Nadson[12], Duerden[13], Chodat[14], Le Roux[15], Lind[16], Bachman[17]. Tous les coraux morts, toutes les formations calcaires côtières ont, plus ou moins, leur couche superficielle cariée et en partie dissoute par les Algues perforantes. J'ai décalcifié des portions de Corail; elles n'étaient qu'un feutrage d'Algues perforantes diverses connues: *Ostreobium* et autres. Toutefois je pense que l'Algue du calcaire côtier dont je viens de parler semble en être une nouvelle que M. Lami, du Muséum de Paris, n'a pas encore déterminée. Il est possible, à mon avis, que ce soit un *Schizothrix*, du même genre par conséquent que les Algues perforantes des calcaires d'eaux douces des lacs de Genève et d'Annecy.

---

[5] Détermination de H. Cannon.

[6] Détermination de E. Wesenberg-Lúnd.

[7] J. S. Gardiner. *The Fauna and Geogr. Maldives and Laccadive Arch.*, Vol. 1, 1902.

[8] Mayor. Some posthumous papers. *Papers Depart. Marine Biology*, 2 et 3, 1924.

[9] Otter. Rock-destroying organisms. *Great Barrier Reef Exped.*, Vol. 1, No. 12, 1937.

[10] Gardiner. *Loc. cit.* et *Proceed. Linn. Soc. London*, t. 143, 1930-31, p. 65.

[11] Bornet et Flahaut. *Bull. Soc. Bot. de France*, t. XXXVI, 1889.

[12] Nadson. *Scripta botanica.* fasc. XVIII, 1900; *Bull. Acad. Sc. de l'U.R.S.S.*, 1932.

[13] Duerden. *Bull. Amer. Mus. Nat. Hist.*, vol. XVI, 1902.

[14] Chodat. *Bull. Herbier Boissier*, t. VI, 1898.

[15] Le Roux. *Annales de Biologie lacustre*, t. II, 1907.

[16] Lind. *Pringsheim Jahr. f. Wiss. botanik*, 32, 1898.

[17] Bachman. *Ber der. Deutsch. Bot. ges.*, 33, 1915.

Examinons maintenant la zone côtière au-delà de la plage: la falaise et le plateau des embruns qui s'étend très loin sur l'îlot.

A première vue, toute la surface de cette zone paraît noire. Tout ce qui est hors de l'eau est noir ou gris sale. Dana l'a bien noté dès 1872[18]. "And they are so blackened by exposure or from incrusting lichens, as to resemble the clinkers of Mauna Loa". En fait ce sont des Algues, surtout cyanophycées, qui recouvrent tous ces rochers jusqu'au moindre morceau de corail ou de pierre quelconque. Ces cyanophycées sont brunes parce qu'elles sont enveloppées d'une production gélatineuse qu'elles sécrètent à la lumière. L'une de ces Algues présente une importance considérable. Si on détache un morceau de corail du sol noir, on s'apercoit qu'en dessous, à l'obscurité, l'Algue est bleue parce qu'elle sécrète peu ou pas de cette substance gélatineuse brune.

Cette Algue est une cyanophycée chroococcale, c'est un *Entophysalis* dont les cellules de 2 à 5 μ sont groupées en petits amas. M. Lami l'a déterminée comme *Entophysalis granulosa* Kützing[19]. Le nom de l'espèce est peut être à revoir car d'autres ont été décrites de Madagacar, des Antilles, du Pacifique. Geitler (1930)[20] dit à son sujet: "très répandue sur les côtes rocheuses de la mer; forme une partie constitutive essentielle de la "zone noire", au-dessus de la limite des vagues".

Si l'on examine à la loupe binoculaire un petit morceau de corail, un petit morceau de coquille de *Turbo* ou de *Tridacne* ou n'importe quel morceau de calcaire de cette zone, on voit d'innombrables petits amas noirs, bruns (bleus s'ils ont été récoltés a l'abri de la lumière). Chacun se trouve dans une petite alvéole plus ou moins grande, plus ou moins profonde qu'il a creusée à partir d'une petite cavité, ou se présente sous la forme de cordons de même couleur, quelquefois ramifiés, dans des galeries jamais closes.

Toutes les surfaces de ces échantillons calcaires sont extraordinairement déchiquetées par cette petite Algue qui reste cepedant toujours exposée à l'air et ne fait tout au plus que s'insinuer plus ou moins profondément dans des anfractuosités préexistantes. Ce n'est pas à proprement parler une Algue perforante. C'est une Algue que j'appellerai "rongeuse" de calcaire.

Lorsqu'on pense aux immenses surfaces qu'elle recouvre dans le monde entier (je l'ai trouvés dans les matériaux rapportés de la mer Rouge par la "Calypso") et qu'après avoir vu son activité microscopique, on constate macroscopiquement que toute l'érosion plus ou moins en cupules, petites ou grandes, de calcaires côtiers dans le monde, est son oeuvre, on est amené à penser que son travail de dissolution du calcaire est considérable.

---

[18] Dana: Corals and Coral islands 1872, p. 178 et 179.

[19] Bornet-Thuret (Notes Algol. t. 1, Paris 1876) ont décrit et figuré une Algue rapportée a cette espece. Mais a mon avis il n'en est rien. L'Algue de ces auteurs est sous-marine, tandis que l'*Entophysalis granulosa* est uniquement dans la zone des embruns. Celle de Bornet-Thuret est un *Geoclapsa*.

[20] Cyanophyceae (Blaualgen) Leipzig, 1930.

[21] Un *Geoclapsa* attaque les calcaire dolomitiques du Tyrol (Bachman, *loc. cit.*)

Elle est partout, aussi bien sur les falaises de Makatea que les "féos" majestueux (restes de 5 mètres de haut d'un ancien récif) de la côte W. de Kaukura, sur toutes les surfaces des îles basses ou hautes. J'ai un morceau de calcaire (coquille de Tridacne avec sédiment consolidé à l'intérieur) récolté dans les racines d'un cocotier. Il est plus ou moins recouvert très légèrement, par endroits, d'humus. Et cependant le sédiment, la coquille, exposés, sont rongés par cette Algue. Je me demande si l'eau douce des pluises ne suffit pas à assurer son activité.[21]

Le travail le plus spectaculaire de cette Algue "rongeuse" de calcaire, c'est la désorganisation des sédiments consolidés dans les fissures desquels elle s'introduit et dont elle sépare les éléments fins ou grossiers. On peut voir également cette activité à la loupe binoculaire. Dans la nature on constate avec quelle facilité on peut séparer à la main les éléments constitutifs d'un sédiment consolidé, attaqué par cette Algue. La vague a peu d'efforts à faire dans ce travail.

Nous pouvons affirmer qu'elle est à l'origine de l'abrasion des sédiments consolidés d'où résultent les immenses et nombreux espaces entre les îlots par où la mer pénètre dans les lagons par dessus le plateau. C'est elle qui, la première, sèpare les éléments consolidés du plateau des embruns.

* * *

Les conséquences de cette observation, d'une Algue dissolvant le calcaire sur terre, dans la zone des embruns et peut être même des pluies aussi bien d'ailleurs que les conséquences de l'activité des Algues perforantes doivent être tirées. Il est bien évident que le problème de la dissolution du calcaire par les organismes vivants animaux ou végétaux sous-marins du plateau côtier ne se présente plus de la même facon. Ce n'est pas l'eau acidifiée par le CO_2 sécrété la nuit par les Algues qui dissout le calcaire. La dissolution ne peut avoir lieu, d'après les faits constatés microscopiquement et macroscopiquement, qu'au niveau même de la paroi externe de l'Algue (et aussi de l'animal) par une sécrètion acide agissant directement sur le calcaire. Les perforations et galeries extraordinairement complexes de notre petite Algue nous montrent que ce phénomène de dissolution est sous sa dépendance directe.

---

[22] *Atoll Research Bulletin*, No. 12, 1952.

On a discuté sur le mécanisme de la perforation des calcaires par les Algues (Duerden, Nadson, Lind, Bachman). Duerden dit que cette action est la même que celle des racines des plantes sur une plaque de marbre, ce qui me paraît exact. On a pensé à la sécrétion par les Algues, d'acide oxalique; mais l'oxalate de calcium est insoluble, ce n'est donc pas possible. Les acides citrique et malique ont des sels solubles dans l'eau. C'est une question qui est à l'étude. En tout cas, on peut dire que c'est un sel organique de calcaire que l'activité des Algues et de certains animaux produit, et qui passe en solution dans l'océan.

Preston Cloud [22] a noté à Onotoa l'existence de la petite Algue bleue dont je viens de parler. Mais il n'a pas soupconné son activité exacte. Il pense qu'elle serait l'agent possible de la formation du "beachrock". C'est le contraire qui a lieu. Elle de détruit.

La consolidation des sédiments ne résulte pas seulement dans la simple précipitation de calcaire entre les éléments voisins . C'est un phénomène tout à fait différent. Il se produit d'ailleurs en profondeur comme en surface. C'est un tout autre sujet sur lequel je reviendrai ailleurs.

* * *

L'aspect en cupules ou cuvettes, résultat de l'activité des Algues lithothamniées aussi bien que des *Entophysalis* peut s'expliquer facilement lorsqu'on suit attentivement leur développement.

La colonie de Lithothamniée apparaît en un point qui s'élargit progressivement. Mais le centre plus vieux et plus épais est plus actif; il creuse davantage le substratum. Des colonies voisines plus ou moins éloignées les unes des autres, font de même et bientôt leur activité se rejoint par les bordures.

L'*Entophysalis* se présente sous forme de petits amas irréguliers, mais le plus souvent groupés, peut-être parce qu'il y a une colonie d'origine qui a essaimé. Les groupes sont plus ou moins éloignés les uns des autres et leur travail sur place aboutit à réaliser un ensemble ayant l'aspect de cupules plus ou moins adjacentes.

* * *

Pour nous résumer, nous dirons que l'activité d'organismes vivants animaux et végétaux perforants ou rongeurs de calcaire est considérable dans la nature et constitue l'agent de base de l'abrasion marine des Iles des Tuamotu et de bien d'autres endroits dans le monde. J'ai mis en évidence deux nouveaux acteurs sur cette scène de destruction: les Lithothamniées marines et les *Entophysalis* de la zone des embruns. Ils sont certainement parmi les plus grands.

Les vues de Gardiner, Duerden, Nadson et autres auteurs, ne font que se développer.

* * *

L'abrasion marine n'a lieu qu'au niveau du battement des marées, aussi bien à l'extérieur, qu'à l'intérieur (côté lagon), et dans le lagon lui-même lorsque les collines et pitons sous-marins ont été soulevés au-dessus du niveau de la mer. Le récif frangeant de Coraux vivants sur la pente extérieure, de 1 à 40 mètres que j'ai examiné attentivement, semble vivre dans un calme relatif car on y voit très peu d'individus arrachés ou brisés. La ligne de 40 mètres de profondeur, lisière inférieure du récif, comporte néanmoins des débris de Coraux qui ont descendu la pente. Mais leur quantité est relativement très faible.

Le calme de la zone de 5 à 40 mètres est bien connu des plongeurs et de meilleurs plongeurs que moi-même me l'ont bien confirmé. Il n'y a pas *d'abrasion marine fondamentale au-dessous de la ligne des marées,* certainement parcè que les perforants et rongeurs de calcaire ne s'y développent pas.

REMARKS ON THE BIOLOGICAL FACTORS UNDERLYING THE DISSOLUTION OF CORAL LIMESTONE IN THE TUAMOTU

By Gilbert Ranson

The Tuamotu Islands are neither recent reefs nor recent atolls. They are constructed out of fossil coral limestone, of *ancient* elevated reefs, on the outer submarine slopes of which only a substantial number of living corals are now showing, that slope being in fact the only part of the island to which the name of "reef" can actually and properly be applied. The so-called reef-flat is only a coastal abrasion shelf, a platform sculptured by sea erosion out of a preexistent mass of hard, rocky, coral limestone.

The outer border of the coastal shelf, where the waves break, is marked by a powerful ridge of calcareous algae. That elevated ridge is the only place where calcareous algae present any important development. Both in the deeper parts, say below 4-5 meters, of the outer slope and on the coastal shelf, calcareous algae are only present as a more or less thin encrustant film.

The surface of the coastal shelf, morphologically speaking, is in fact remarkably uneven in its minor features. A great number of excavations or tidal pools are densely lined with calcareous algae, the irregularly attacked limestone giving very strongly the impression of suffering from some kind of organic necrosis.

Leaving aside the much more limited action of the sea-urchins, the facts observed lead to the supposition that the alveolisation and dissolution of the limestone may thus have its main origin in the action of the calcareous algae.

A first study was then made of the progressive destruction of the limestone of a dead colony of an astraeid coral by the alga *Porolithon onkodes.* All phases of the attack and of the progressive destruction of the spines as the septa, then of the septa themselves and finally of the whole calyx can be observed by direct observation.

It seems therefore highly probable that the destruction of the coastal shelf is largely due to the dissolution of limestones under the direct influence of calcareous algae. At least under the low water mark.

Above the low water mark a major role seems to be played by different lithophagous animals, such as *Lithotrya nicrobarica* and a new species of *Physcosoma,* to which sponges like *Cliona* may be added.

On the coastal shelf all the salient asperities are deeply attacked by a boring alga belonging to Cyanophyceae: *Ostreobium* or, more likely, a new *Hyella* whose identification is not yet complete.

So much for the head itself. If we now look on the cliff and farther inland as the plateau or more preciously on that part called in French the "plateau des embruns," the "spray plateau," the whole region appears black or grey. There again the main agent of the attack is an alga, belonging to the Chroöcoccales, *Entophysalis granulosa* as identified by Dr. Lami. Any piece of limestone, of dead coral, of shell, be it *Tridacna* or *Turbo,* in that particular zone shows numerous small dark spots located in the more or less deep cavity the alga has apparently dug.

Such algae are very widely distributed, and it may be thought that the result of their action, in the alveolisation and destruction of coral limestones, may be a tremendous one, and in many places in the world.

Their main action lies, however, probably in the disorganisation of hardened and compact sediments, into whose cracks and fissures they readily penetrate and whose constituent elements, coarse or fine, they separate. The sediment thus loosened, having lost its compacity is an easy prey to the destructive mechanical impact of the waves.

Conclusion of such observations are following. The dissolution of the limestone through organic action is not caused by the CO_2 liberated at night by plants, but by the direct contact action of specific algae whose acid secretions dissolve the rock.

The exact mechanism of the chemical action of algae has not yet been fully elucidated. Different hypotheses have been proposed.

Some authors have recently considered these small alga to be possible agent in the formation of the head rock. Foı me, it is exactly the contrary which happens. The alga does not construct, it destroys.

In summary: the activities of organisms able to dissolve or perforate the limestones are extremely important. They seem to be with the Tuamotu the main agent of the formation of the coastal shelf. And the same fiction is probably true for many other regions of the world.

Marine abrasion is only active in the tidal zone. The deeper region, from 5 to 40 meters, where the living corals thrive, is calm but if there is no important marine abrasion below the low water mark, it is certainly prominently due to the fact that limestone dissolvent and destructive organisms are absent in that particular zone.

OBSERVATIONS SUR LES ILES BASSES DES TUAMOTU (OCEANIE FRANCAISE)

Par Gilbert Ranson
Muséum National d'Histoire Naturelle de Paris, France

Darwin est passé rapidement aux Tuamotu et dit à leur sujet: "plusieurs de ces couronnes de terres coralliennes, des plus curieuses, s'élevant juste au-dessus de l'eau, qui ont été appelées des îles à lagons . . . . Du haut du mât, une large étendue d'eau calme peut être vue à l'intérieur de la couronne. Ces îles coralliennes basses et creuses en leur centre, n'ont aucun rapport avec le vaste océan extérieur duquel elles s'élèvent d'une manière abrupte et il semble étonnant que de si faibles "invaders" ne soient pas submergés par les toutes puissantes et incessantes vagues de ce grand océan, mal appelé Pacifique".[1] Darwin n'a rien dit de leur origine. Mais sur sa carte il les figure en bleu comme étant toutes des atolls vivants, actuels et dit-il, plus tard, situées de ce fait, dans une zone d'affaissement du Pacifique.

Les premiers voyageurs qui out visité effectivement ces îles n'ont pu admettre que cette règle s'appliquât à Makatea et Niau entre autres.

Pour Dana [2] les îles de l'archipel des Tuamotu n'ont que la hauteur des matérieux accumulés par l'océan. Rien n'indique qu'une élevation y soit en cours. Ces îles doivent exister depuis fort longtemps dans l'état où elles sont présentement. Sur ce point il est d'accord avec Darwin. Mais s'il ne constate pas d'élévation générale, il ne parle cependant pas d'affaissement possible. Il dit, au contraire, qu'elles sont plutôt dans un état stationnaire. Mais, dit-il, il existe quelques cas particuliers d'élévation "however, some of which are of unusual interest.": Honden (ou Henuake), Dean's Island (ou Nairsa), Aurora (ou Metia, maintenant Makatea) et Clermont-Tonnerre.

Mais Couthouy, en 1841 [3], avait éclairé la question d'une lumière toute spéciale. C'est que Couthouy a vécu de longs mois sur un grand nombre des îles de l'Archipel. Il parvient, dit-il, aux mêmes conclusions que Darwin au sujet de leur origine par affaissement d'anciennes îles, mais il ne soutient pas ses opinions concernant les zones limitées et définies de l'affaissement et de l'élévation.

---

[1] *Journal of Researches.* London, 1840.
[2] U. S. Expl. exped., Geology, 1849, p. 402.
[3] *Journal Nat. Hist.* Boston, 1843-1844, vol. IV.

Les conclusions auxquelles il a été amené à la suite de toutes les observations qu'il a faites en Polynésie, sont résumées par lui, comme suit:

1°) L'affaissement ne fut pas continu, mais il fut interrompu pendant de longues périodes durant lesquelles la terre, et après sa disparition, le récif, restèrent stationnaires et des terrasses successives se formèrent;

2°) L'affaissement a continué, au moins dans certains endroits et jusqu'à une époque relativement récente, pour cesser ensuite peu de temps après la submersion de la terre pré-existante;

3°) Puis a suivi un intervalle de repos fort long, avec le récif à une profondeur suffisante en dessous de la surface de l'océan, pour permettre aux Polypes de construire le récif dont les fragments sont maintenant répandus sur le plateau supérieur;

4°) *Cet état de repos a été suivi d'un soulèvement durant une période pendant laquelle le récif était considérablement plus bas que ne l'est le sommet actuel et que, exposé à la pleine violence du ressac, il fut mis en pièces et les fragments transportés à leur place actuelle;*

5°) *Ce processus de soulèvement se poursuit encore, non seulement dans les groupes coralliaires, mais aussi dans la plupart des iles volcaniques de Polynésie.*

En 1903, Agassiz[4] exprime ainsi son opinion: "L'archipel des Tuamotu est constitué de plus de 70 atolls dont beaucoup sont de grandes dimensions *et ont des îles soulevées composées de calcaire corrallien. Les atolls les plus bas ont été réduits par la dénudation et l'érosion sous-marine d'îles élevées . . . . jusqu'à ce que le rebord terrestre soit réduit au niveau qu'il occupe maintenant.* Les stades successifs de dénudation et d'érosion sous-marine sont représentés par des îles comme Makatea, Niau, Rangiroa, Hao et d'autres. Quelques-uns des atolls les plus à l'Est des Tuamotu sont chétifs et de tels atolls sont, comme Pinaki, Nukutipipi, Anu-Anurunga, Anu-Anuraro, d'admirables abrégés de la structure des plus grands."

Puis plus loin: *"De sorte qu'il n'est pas étrange de considérer la zone des Tuamotu, comme je suis incliné à le faire, comme résultant d'une élévation; la terre ayant été soulevée fut affectée de la même manière, par dénudation et érosion, que l'ont été les masses de calcaires coralliens soulevés des Fidji.* Toutefois il semble y avoir eu, d'après les faits évidents présentés, une beaucoup plus grande uniformité dans la hauteur d'élévation des Tuamotu . . . . De telle sorte que je suis, jusqu'à un certain point, justifié quand je nie que les Tuamotu soient situées dans une zone d'affaissement et que cet affaissement ait été le grand facteur, comme le soutiennent Darwin et Dana, de la formation des atolls caractéristiques de ce groupe."

---

[4] *Mem. Mus. Comp. Zool.*, vol. XXVIII, 1903.

Pour Agassiz, ces masses coralliennes soulevées, ont été l'objet de la dénudation et de l'érosion; le lagon central en serait la résultante. On se demande pourquoi ces facteurs n'auraient laissé partout que des couronnes proéminentes. Certes l'érosion est importante. On voit bien son oeuvre, mais il est impossible de lui imputer les lagons quels que soient les phases par lesquelles sont passées ces îles au cours de l'histoire sol des îlots.

D'ailleurs l'idée que Makatea et . . . . disons Hikueru ou toute autre ile basse, ne représentent que les stades ultimes d'un même phénomène, nous paraît de toute évidence, erronée. Mais Agassiz avait raison quant au soulèvement.

Darwin dans "Les récifs de Corail" essaie de réfuter les arguments de Dana et de Couthouy. Il persiste à croire que les îles des Tuamotu sont des atolls, vivants actuels, stationnaires au niveau de l'eau, sur lesquels la mer rejeterait, sable, pierres, masses coralliennes, constituant le de la terre.

Il persiste à penser que les Tuamotu sont dans une zone d'affaissement et qu'il n'y a pas eu d'exhaussement du sol. Cependant, il admet que pendant un certain temps, ces atolls sont restés au même niveau. Il préfère accepter l'hypothèse d'un abaissement du niveau de la mer, pour le cas où les observations de Dana et Couthouy s'avéreraient exactes.

- - - - - - - - - - -

Lorsqu-on se trouve seulement devant les 80 mètres de calcaires coralliens soulevés de Makatea et que l'on sait que les Coraux de récifs ne vivent plus à partir de 40-50 mètres (ce que j'ai bien constaté à Hikueru), on est bien obligé d'admettre, comme Darwin, que ces énormes couches de calcaires coralliens (que l'on sait beaucoup plus épaisses sous l'eau, depuis les grands sondages récents) n'ont pu se former qu'au cours d'un affaissement lent du sous-sol, à la vitesse de croissance des Coraux. L'affaissement a dû certainement se faire par périodes entrecoupées de temps d'arrêt, voire même de soulèvements, comme nous l'indiquent les zones alignées d'excavations de la falaise de Makatea.

D'autre part la forme extrêmement irrégulière, la direction générale variée, des îles des Tuamotu, nous obligent à admettre, entre autres, que la forme générale de l'ancien atoll vivant, n'est pas le fait de l'action des vents dominants, mais bien du socle sur lequel s'est développé le récif à l'origine. Nous sommes donc amenés à considérer que ce socle n'est pas un plateau sous-marin, mais bien une île, comme le suppose Darwin. Ces deux faits étant admis, nous devons tout naturellement, penser que Darwin a raison dans son explication de la formation d'un atoll.

Mais il faut bien reconnaître que, dans le détail, il semble y avoir quelques modifications à apporter au schéma de Darwin. Celle de Couthouy, en premier lieu, concernant les zones de soulèvement et d'affaissement est parfaitement justifiée.

- - - - - - - - - - -

Avant de poursuivre ces critiques il me faut résumer brièvement les conclusions auxquelles je suis parvenu après mon séjour de 8 mois dans les Tuamotu.

Sans aucun doute possible, toutes les îles des Tuamotu ont subi un soulèvement récent, que l'ont peut dater du quaternaire, car des Mollusques actuels: *Tridacna* et *Turbo*, sont consolidés avec des blocs de Coraux, appartenant également aux mêmes espèces que ceux vivant actuellement sur la pente extérieure. Les *Tridacna* et les *Turbo* consolidés dans le corail fossile se retrouvent aussi bien sur le sommet de la falaise de Makatea que sur le bas plateau des embruns d'Hikueru, de Takume, de Takaroa, Takapoto, Fakarava, Apataki, Anaa, Rangiroa, Niau etc . . . . Nous ne sommes donc pas en présence de divers niveaux d'érosion mais de différents niveaux d'exhaussement.

Makatea s'est élevée de 100 mètres au-dessus de l'eau, Niau de 5 mètres, les autres de 3 à 4 mètres. Mais leurs surfaces, où croissaient brillamment les Coraux, devaient être de 10 à 20 mètres sous l'eau. Il faut ajouter ces chiffres aux précédents pour avoir la valeur approximative du soulèvement.

L'uniformité de la hauteur, au-dessus de l'eau, de 78 îles, attire tout de suite l'attention. Je pense qu'au cours de la longue histoire de leur formation et de leur croissance, tous les atolls étaient parvenus au même niveau sous-marin. Le "plateau" sous-jacent des Tuamotu se serait soulevé alors tout entier. Les deux îles de Makatea et de Niau se trouvant en bordure, ont été soumises à une poussée spéciale.

Nous devons tirer tout de suite une conséquence du fait que tous les atolls ont été soulevés. Les îles basses des Tuamotu ne sont donc pas de récifs, ni des atolls actuels, même stationnaires. Ce sont des "terres", des îles, tout simplement.

Ce sont maintenant des socles de calcaire corallien fossile, sur les pentes sous-marines desquels se développent de nouveaux récifs frangeants, vivants, actuels, comme il s'en est développé à l'origine sur n'importe quel socle. Ces derniers sont les seules formations auxquelles on puisse accorder le nom de récifs; tout le reste est du calcaire corallien fossile. Il est par conséquent absolument erroné de désigner sous le nom de "pente du récif", de "plateaur récifal" (appelé aussi "récif frangeant"), et de "récif", les divers éléments de ces îles. Il ne s'agit en fait, respectivement, que de la pente du socle de l'île du plateau côtier d'abrasion et du socle de calcaire corallien fossile dont est constituée l'île. Prenons un exemple: près de La Rochelle, en France, existe, une falaise constituée de calcaire corallien jurassique; la mer l'a fait reculer et un plateau en résulte. On ne parle ni de récif, ni de plateau récifal pour les désigner! On pourrait en citer bien d'autres.

Il ne s'agit pas uniquement de modifications de termes. C'est beaucoup plus important. Il s'agit d'une manière différente de voir les faits. Et les conséquences en sont appréciables. Il ne faut pas essayer, dans une tentative désespérée, de "sauver", si je puis dire, le terme de récif en lui donnant le sens d'écueil, car on devrait appeler récifs toutes les îles basses du globe. D'ailleurs ce serait en contradiction avec le sens que lui donnait Darwin qui croyait que son récif frangeant et son récif barrière étaient des choses bien vivantes, actives présentement.

- - - - - - - - - - -

Immédiatement après leur émersion, la mer s'est attaquée à ces nouvelles "terres" basses et les a falaisées.

Elle a abrasé assez rapidement les zones de sédiments consolidés et par là pénètre journellement dans le lagon, par dessus le plateau résultant, plus ou moins large. Les blocs récifaux consolidés ont résisté davantage et ce n'est que très lentement qu'ils sont abrasés. Il en subsiste des îlots. La mer aussi bien du côté lagon que du côte océan, accumule sur eux du sable et des pierres. La végétation s'y est instalée.[5]

Tout au début, la mer déferlait presque jusqu'au sommet de ces îlots ou rochers coralliens peu élevés, et elle a constitué, presque sur le sommet, une première plage, avec digue (rempart) de morceaux de coraux roulés. On retrouve partout dans les îles basses, cette première plague avec digue naturelle subfossile. Je l'ai remarquée même, pour la première fois, à Aitutaki aux îles de Cook. Elle est à 1m, 50 environ de dénivellation par rapport à la place actuelle. Je reviendrai sur ce sujet.

Mais, en même temps, à la limite du bas d'eau, sur le bord du plateau, au niveau où battent les vagues, se développaient rapidement les Algues calcaires lithothamniées. Elles ont créé là, une formation sous-marine de près de 5 mètres de hauteur, sous-marine par endroits. Je l'ai observée en me baignant avec un masque à glace, sur de grandes distances à Hikueru et à Takume. Sa puissance et son efficacité me sont apparues lors d'une grosse houle du Sud. D'énormes vagues venaient frapper cette falaise vivante d'Algues lithothamniées, et étaient projetées perpendiculairement à une dizaine de mètres ou davantage. Les vagues ainsi amorties[6] viennent déferler sur le plateau côtier où elles perdent encore de leur force, pour aboutir à la nouvelle plage qui se trouve de quelques mètres à une centaine de mètres (ou plus) de cette bordure, selon les conditions locales. Une digue actuelle de sable ou de morceaux de corail roulés, haute de 1 m. ou 2 m. y a été constituée. Elle est juste au-dessus de ce qu'on doit encore appeler la falaise bien qu'ici cette dernière soit souvent fort basse. A Makatea et Niau la falaise est spectaculaire, mais dans les îles basses, j'ai mis beaucoup de temps à me rendre compte de son existence et pourtant c'est cette notion, une fois acquise, qui m'a permis de voir plus nettement certains phénomènes.

---

[5] Mais il existe aussi a Takume, par exemple des ilots formés d'amas de sable et de pierres que la mer accumule depuis peu sur le plateau cotier abrasé de la cote Est de cette ile. Ce phénomene se développe sous nos yeux vers la pointe Sud et menace de fermer totalement le lagon de ce coté.

Cette petite falaise a reculé sans cesse laissant entre elle et la bordure initiale, un plateau plus ou moins large, résultant de l'abrasion de la portion marginale de l'île, au niveau de la basse mer.

C'est un plateau côtier, comme la mer en fait sur tous les bords des continents qu'elle attaque. Ici c'est une masse de corail fossile qu'elle détruit, achevant en fait, l'oeuvre d'organismes vivants, perforants, rongeurs de pierre. Des blocs, de toutes tailles, en continuité avec le substratum y subsistent, témoins de l'ancien niveau. Il ne faut pas les confondre avec ceux que la mer y rejette, les arrachant à la bordure. Ces derniers ont, le plus souvent, la marque de leur origine: ils ont une couche épaisse de Lithothamniées. Il est invraisemblable de donner le nom de "plateau récifal" et encore plus celui de "récif frangeant" à cette formation comme le font les auteurs. D'autant plus que ce plateau est le plus souvent désespérément désertique en ce qui concerne les Coraux.

- - - - - - - - - - -

La mer n'attaque bien le socle qu'au niveau de la marée, où battent les vagues. Au-dessous, de 5 à 40 mètres, il semble règner un calme relatif car les Coraux vivants, comme j'ai pu m'en rendre compte, ne paraissent pas du tout souffrir des ondulations de la mer. Les plongeurs le savent bien. On peut affirmer qu'en principle l'abrasion marine n'est importante qu'au zéro, sauf lorsqu'il existe une falaise sous-marine où l'attaque de la vague produit son effet; mais pas au-dessous d'une zone où les perforants ou rongeurs de pierre sont actifs. Lors des grandes tempêtes, la mer n'arrache que des blocs déjà déchiquetés de la bordure du plateau. Elle les transporte plus ou moins loin sur ce dernier.

---

[6] Elles le sont d'autant plus que cette masse d'Algues calcaires n'est pas homogene mais creusée d' innombrables trous par suite de la croissance désordonnée de ces Algues. L'eau pénetre en grande partie dans ces trous qui communiquent souvent avec la surface extérieure.

- - - - - - - - - - -

En arrière de la falaise et, par suite, après et sous la digue actuelle, nous avons ce que nous pouvons appeler le plateau des embruns et enfin la digue sub-fossile, puis le sommet de l'île.

Entre les deux digues (remparts) actuelle et sub-fossile j'ai dit précédemment qu'il y avait une dénivellation de 1m, 50 environ. J'ai pensé, dès l'abord, qu'il y avait eu soit un soulèvement général correspondant, soit un abaissement du niveau de la mer. Mais les faits observés à Takume, au village de Tahéto, m'ont démontré que le phénomène pouvait s'expliquer d'une manière beaucoup plus simple. Là, la pente extérieure de l'îlot est plus faible et la digue de Lithothamniées, moins épaisse, est moins efficace.

La mer déferle très fréquemment jusqu'au sommet de l'île où se trouve la digue (rempart) unique. J'ai pensé alors que si la digue à Lithothamniées de Hikueru n'était pas si puissante, elle n'amortirait pas, comme elle le fait, le choc des grosses vagues que parfois malgré tout, envahissent le sommet de l'îlot lui-même, comme ce fut le cas une fois lorsque je m'y trouvais. Alors la digue serait toujours où elle fut à l'origine. D'ailleurs au cours des grosses houles de juin-août 1952, la digue actuelle a été en plusieurs points défoncés et en certains autres transférée totalement à plusieurs mètres en arrière.

Les faits signalés par Cloud[7] ne pourraient-ils pas s'expliquer également par des conditions locales?

- - - - - - - - - - -

La masse formée sur la bordure par les Lithothamniées, n'est pas homogène dans l'espace. Elle est coupée d'anfractuosités, de chenaux plus ou moins étroits, jamais bien larges. Vue d'avion cette bordure de l'île, apparaît formée d'encoches et de promontoires, véritable feston. C'est le reflet, très exagéré par les masses d'Algues calcaires, de l'irrégularité de la paroi de la pente sous-marine extérieure. Je m'en suis bien rendu compte en la longeant extérieurement. J'ai observé aussi que les véritables fjords de la falaisse sous-marine, hauts de 5 mètres environ, plus ou moins profonds, plus ou moins larges avaient leurs parois grises, mais absolument dépourvues de Coraux. Ces fjords apparaissent désertiques. Est-ce parce que la lumière y est plus rare? J'ai pensé que les caps et les baies de cette paroi sous-marine, pouvaient être le fait de l'hétérogénéité du socle corallien consolidé présentant des zones plus ou moins résistantes à l'action des vagues. C'est la comparaison de cette falaise avec la falaise aérienne qui m'a donné cette idée. Mais nous savons que la falaise aérienne n'est pas que le résultat de l'action des vagues, mais avant cela, de l'activité d'Algues et d'Animaux perforants. C'est pourquoi j'ai soupconné que la sculpture de la falaise sous-marine pouvait bien être l'oeuvre des Lithothamniées. Mais cette hypothèse reste à vérifier. Je ne me suis tout de même pas assez aventuré dans ces fjords pour constater si leur couleur spéciale provenait du fait qu'ils seraient tapissés d'une pellicule de Lithothamniées.

---

[7] *Atoll Research Bulletin*, n° 12, 1953.

- - - - - - - - - - -

J'ai dit que la mer abrasait la côte des îles sur lm, 50 environ d'épaisseur à la position actuelle de la falaise, les zones de sédiments consolidés ayant d'abord été complètement supprimés, les îlots plus résistants étant menacés eux aussi de l'être, à plus ou moins longue échéance.

Mais examinons attentivement la composition de la portion de l'île que la mer détruit. Nous en avons les restes sur le plateau des embruns depuis la falaise actuelle jusqu'au sommet de l'îlot. Dana en 1872 en donne le tableau suivant: "The emerged land beyond the beach, in its earliest stage, when barely raised above the tides, appears like a vast field of ruins. Angular masses of coral rock, varying in dimensions from one to a hundred cubic feet, lie piled together in the utmost confusion; and they are so blackened by exposure, or from incrusting lichens, as to resemble the clinkers of Mauna Loa; moreover, the ring like metal under the hammer. Such region may be traversed by leaping from block to block, with the risk of falling into the many recesses among the huges masses . . . . Some of the blocks, measuring five or six feet in each of their dimensions, were portions of single individual corals; while others has the usual conglomerate character of the reef-rock, or, in other words, were fragments torn by the waves from the reef rock." [8]

Toute la zone du plateau côtier jusqu'au trottoir à Lithothamniées était constituée de la même manière avant d'être abrasée. Las "témoins" qui en subsistent sur le plateau, l'indiquent bien, non seulement par leur composition, mais aussi par leur niveau: le sommet des plus hauts est exactement au niveau du sommet de l'îlot. Il subsiste des "témoins" de toutes tailles et de toutes dimensions.

---

[8] Coral and Corals Islands, 1872.

Ce plateau des embruns, noir parce que recouvert d'Algues "rongeuses" de calcaire et autres, a été quelque peu érodé au début du soulèvement lorsque le plateau côtier n'était pas, ou peu, amorcé.

Mais le tableau que nous avons là sous les yeux, bien que très légèrement vieilli et que décrit si magnifiquement Dana, est celui-là même de ce que fut un récif très riche composé d'individus coralliens volumineux serrés les uns contre les autres, s'enchevêtrant d'une manière plus ou moins inextricable. Il suffit d'avoir plongé dans certaines zones des côtes de la Nouvelle-Calédonie, où les récifs sont si riches, pour le comprendre.

Maintenant c'est une masse de blocs de Coraux fossiles, quaternaires, restés en place et peu consolidés.

Ce ne sont pas du tout des matériaux rejetés là par la mer lors des tempêtes. On en retrouverait des restes sur la pente extérieure, sous l'eau. D'ailleurs ils ne seraient pas disposés du tout comme ils le sont. Ils formeraient des amas, comme les digues ou remparts. Il n'y a pas de discussion possible, ils sont en place. Sur la pente extérieure nous avons bien les mêmes espèces, mais l'ensemble du récif vivant n'est qu'une miniature insignifiante de ce que nous avons sous les yeux à l'état fossile, sur le sol de l'île. C'est une formation nouvelle, récente.

Ce récif corallien commence avec le trottoir à Lithothamniées; la formation marginale importante qu'elles construisent fait réellement partie du récif. De là il s'étend qusqu'à 40 mètres environ comme j'ai pu l'observer à Hikueru et Takume. A la limite inférieure, on observe quelques débris roulés de Coraux; leur couleur blanche les rend très apparents.

Le récif y est constitué d'individus de volume très restreint. Les plus gros sont ceux des Millépores verts et d'un *Acropora* en immenses éventails. Mais partout, on voit le socle entre les individus coralliens. Il n'y a pas cette intrication extraordinaire des inividus comme on l'observe en Nouvelle-Calédonie, même dans le lagon, et encore moins comme l'était, au quaternaire, le récif dont nous avons les restes sur les bords des îlots. Le volume des éléments de ce dernier indique qu'il prospérait au moins sous 10 à 20 mètres, peut-être davantage. En effet les Coraux croissant à moins d'un mètre sous l'eau sont peu volumineux; ils sont aplatis, quelquefois même encroûtants.

Dans les Tuamotu, le récif vivant, actuel, est peu de chose à côté de ceux qui ont construit ces immenses masses calcaires, du crétacé au miocène, et dont les falaises de Makatea nous donnent une idée. A l'heure présente, en cela je suis tout à fait d'accord avec Crossland, les forces de destruction sont considérablement plus grandes dans les Tuamotu que les forces de construction. Mais l'histoire, inscrite dans les falaises de Makatea nous laisse supposer que ce n'est qu'une période intermédiaire, momentanée, à laquelle succèdera une nouvelle période d'affaissement avec un nouveau développement luxuriant des Coraux. A condition bien entendu que les événements se succèdent dans l'avenir comme dans le passé! Ce qui n'est pas absolument certain.

- - - - - - - - - - -

En général, le plateau n'est creusé que de Om, 30 environ. C'est un immense désert en ce qui concerne le corail. Mais quelquefois, par suite d'anfractuosités dans la bordure du trottoir ou par suite d'une abrasion plus profonde dans une zone de sédiments consolidés, il y persiste, à marée basse, 0m, 80 à 1m, 50 d'eau. Dans ce cas les Coraux "remontent" si l'on peut dire, de la pente et croissent dans ces zones. Mais ce ne sont que des individus courts, aplatis, quelquefois encroûtants, méconnaissables; ils sont très dispersés. On ne peut pas dire que l'ensemble constitute un "récif" composé de quelques individus dispersés. Ce sont plutôt des "évadés" du vrai récif extérieur. On y trouve le plus souvent des *Acropora* et des *Porites.* Il y a bien quelques Astréidés mais ils restent très rudimentaires.

Il serait intéressant d'étudier de près, ce que je n'ai pas eu le temps de faire, cette évasion, du vrai récif de la pente extérieure (où toutes les conditions sont maxima pour la croissance du Corail) de formes qui parviennent à subsister dans les zones ennoyées du plateau, ou à se développer plus ou moins dans les lagons, qu'ils soient sans passes ou avec passes. Nous assistons là à la mise en évidence de réactions physiologiques un peu différentes de groupes coralliens divers. Dans les lagons sans passes, ce sont les Porites qui dominent et acquièrent un développement important. Ce sont eux surtout qui recouvrent les pitons et collines sous-marines. Dans les lagons "à passes", il y a aussi de nombreux *Acropora* branchus.

- - - - - - - - - - -

J'ai dit précédemment que le récif vivant, actuel, débute au trottoir à Lithothamniées. Il est extrêment important de noter que cette formation d'Algues calcaires prend son plus fort développement à l'endroit où battent les vagues, à marée basse, mais également qu'elles ne se développent jamais sur les Coraux vivants, mais toujours sur un socle mort, fossile. Or, pour que ce socle soit à fleur d'eau ou découvert à marée basse, il faut absolument qu'il soit là non pas par suite d'un simple stationnement du niveau du récif vivant, mais bien par l'effet d'un soulèvement de tout le socle ancien. On mesure les conséquences d'un tel fait. Tous les trottoirs à Lithothamniées sont sur des socles fossiles soulevés et plus ou moins abrasés. Mais alors ce qu'on appelle récif barrière n'est rien d'autre qu'un ancien récif frangeant soulevé et abrasé. D'ailleurs la distinction entre le "récif frangeant" et le "récif barrière" des auteurs est très difficile. C'est ainsi que Davis[9] dit: "When a reef of the fringing kind fronts the open ocean it repeats the features of barrier reefs so closely that, except for the absence of a lagoon, its description may be taken from theirs, as given below."

Effectivement, à Tahiti, le "récif barrière" est tantôt avec, tantôt sans lagon côtier. Dans les deux cas comme pour ce que les auteurs appellent "récif frangeant", il s'agit du plateau côtier d'abrasion d'un socle soulevé.

Pourquoi, dans certains cas, est-il creusé et possède-t-il un lagon et dans d'autres est-il sous excavation. Je crois l'avoir compris quand je suis allé de Suva à Nandi aux Fidji, en avion.

J'avais fait la connaissance d'un pilote du centre d'aviation, parlant le francais. Je lui ai expliqué ce que je venais faire dans le Pacifique et ce qui m'intéressait. Il en a entretenu le pilote de l'avion faisant le service et étant seul comme passager, ce pilote que je ne saurais trop remercier, m'a fait suivre toute la côte, à basse altitude.

J'ai pu constater que la configuration du terrain se poursuit sous l'eau. Par exemple une zone de petites collines avec vallées se poursuit sous la mer où l'on distingue très bien les vallées bleues plus ou moins profondes et les petites collines à sommets blancs plus ou moins abrasés. Une zone plate se poursuit sous l'eau par un plateau sans relief. Une zone falaisée a un plateau côtier sous excavations.

Ainsi les caractères du lagon côtier de la baie de Papeete du district de Faaa, qui a même un chenal important, résultent sans aucun doute de la configuration du sous-sol de cette zone. En bien d'autres endroits de la côte il n'y a pas de lagons côtiers. On peut en dire autant de l'immense lagon côtier de Nouméa.

Ici encore le vrai récif frangeant, vivant, actuel, commence avec la digue ou trottoir à Lithothamniées et se poursuit en profondeur sur la pente de l'ancien récif frangeant soulevé.

Il est nécessaire de noter cependant que dans les lagons côtiers de ce qu'on appelle les "récifs barrières" se développent des formations coralliennes spéciales qui sont dans certains cas assez propères. C'est ainsi que dans le lagon de Faaa à Papeete il y a, outre des *Acropora*, deux espèces de Coraux, qui se satisfont d'eaux très chargées par instants en sédiments. L'ensemble est très actif et on peut admettre qu'il parviendra à combler en partie ce lagon.

---

[9] The Coral reef problem. *Amer. Geogr. Soc. sp. publ.* n° 9, 2428.

A Nouméa il y a aussi par endroits, dans le lagon, de beaux récifs vivants, actifs, et les pentes de chaque îlot sont couvertes de récifs frangeants actuels. Grâce à M. et Mme Catala j'ai pu en observer quelquesuns. Le lagon de Nouméa est immense; c'est une véritable mer intérieure; c'est pourquoi on y trouve d'assez nombreuses espèces de Coraux, mais ils ne donnent tout de même naissance qu'à des formations très secondaires.

Les pentes de l'îlot du Porc Epic, dont j'ai fait le tour à la nage avec un masque, présentent de beaux échantillons coralliens, mais ils sont encore dispersés. Ce n'est pas une formation puissante ni surtout ancienne. Elle est récente; elle a pris naissance aprés le soulèvement quaternaire.

- - - - - - - - - - -

Si, après ces considérations, nous examinons la carte de la Planche I du livre de Darwin "Les Récifs de Corail" nous sommes amenés à conclure que tout ce qui est en bleu ne représente que des plateaux côtiers d'abrasion d'atolls fossiles soulevés ou les bordures de récifs frangeants fossiles soulevés et abrasés. Mais, dans ce dernier cas, la ligne bleue représente aussi le trottoir à Lithothamniées, point de départ du récif frangeant, vivant, actuel, qui se développe sur la pente extérieure.

- - - - - - - - - - -

La couche de Coraux quaternaires du sol de l'île d'Hikueru, aux Tuamotu, peut être considérée comme ayant eu approximativement 3 mètres d'épaisseur. Sous cette couche, il y a une dalle calcaire très consolidée qui paraît être miocène ou pliocène. Ainsi, toute l'énorme épaisseur de ces îles, que Makatea nous laisse soupconner, se serait formée du crétacé, peut-être, au pliocène. L'activité des Coraux, même au quaternaire, a été beaucoup plus grande qu'elle l'est actuellement dans ces régions. Les eaux devaient y être plus chaudes. Aujourd'hui ces îles sont à la lisière orientale de la mer de Corail et les courants d'eaux froides venant de l'Est et du Sud-Est s'y font certainement sentir. Les cartes de perturbations saisonnières de la température des eaux nous indiquent qu'une "langue" d'eau froide atteint les Malden et même les Gilbert.

- - - - - - - - - - -

Du côté lagon il y a aussi un plateau côtier d'abrasion, mais plus court, avec une plage de sable. Puis assez brusquement du côte au vent de l'îlot, on atteint des fonds de 20 mètres. La pente est plus douce du côté sous le vent. J'ai fait près de 300 sondages au plomb dans le lagon d'Hikueru; je m'y suis baigné avec le masque à glace et j'y ai plongé.

Le lagon d'Hikueru ne dépasse pas 38 mètres de profondeur en son centre. On a en somme une pente plus ou moins rapide jusqu'à 30 mètres. Après il y a comme un immense plateau central de 30 à 38 mètres.

D'un fond de sable blanc qui recouvre tout, s'élèvent des collines et des pitons sous-marins très nombreux. Leurs pentes sont plus ou moins abruptes, quelquefois verticales. Ils sont constitués d'un socle fossile qui a subi, comme toute l'île, le soulèvement quaternaire; les sommets de beaucoup d'entre eux ont émergé, puis ils ont été abrasés. Il reste, par endroits, des témoins de l'ancien niveau. J'ai examiné attentivement beaucoup de ces plateformes abrasées à 0m, 60—0m, 80 sous l'eau. Certaines sont très larges, aussi larges que des îlots côtiers, c'est-à-dire qu'elles ont de 100 à 500 m. et plus.

Sur ce socle ancien croissent surtout les Porites. Il y a bien quelques *Acropora* et des *Astréides,* mais très rarement et rabougris dans les lagons sans passes.

La pente sous-marine du lagon du côté sous le vent, est abrupte. C'est comme la paroi d'un "mur" (légèrement couverte de sable), qui doit se prolonger directement sous le sable de la ligne de 20 mètres de profondeur. Nous pouvons ainsi très bien nous représenter la bordure de l'ancien atoll que nous embrassons totalement maintenant depuis la pente extérieure jusqu'à la pente intérieure.

Certes, il y a certainement eu, à l'intérieur, sur les bordures du lagon, apport de gros blocs coralliens rejetés par la mer, du plateau côtier. Mais sans aucun doute les collines et pitons sous-marins du centre du lagon sont en place et se sont accrus à partir d'une base qui est fort loin en profondeur. La coupe d'une colline du lagon, est, à mon avis, exactement semblable à celle de la bordure océanique de l'île et je pense que son origine est la même.

L'abrasion, dans le lagon, n'a atteint que les portions émergées. Par ailleurs, on ne constate qu'un remplissage progressif par le sable. La théorie d'Agassiz ne peut donc être retenue.

Les faits ainsi constatés nous amènent à apporter cependant de sérieuses modifications au schéma de Darwin. Le phénomène fondamental de la subsidence ne saurait, de toute évidence, subir la moindre retouche.

Si nous considérons la figure 5, p. 149 de l'édition francaise de 1878, "Les Récifs de Corail", nous constatons que sur al ligne A' C B', Darwin figure des cocotiers et un chenal de lagon. Ceci prouve que nous sommes en présence d'un récif frangeant, soulevé et abrasé, le chenal n'étant que très accidentel et dépendant de la configuration du sous-sol d'origine. Dans la figure 6, page 152 en A″ C′ A″ nous aurions un atoll avec lagon au centre. Cette figure ne peut absolument pas représenter un atoll. En rejoignant par une horizontale les points A″ A″, légèrement déplacés au-dessous de la ligne du niveau de la mer, nous avons alors un schéma, de la paroi marginale seulemént, d'un véritable atoll vivant, à surface active ou encore celui d'une collines ou piton sous-marins du lagon.

Si nous placons les deux points A″ A″ un peu au-dessus de la ligne du niveau de la mer et que nous les rejoignions par une ligne légèrement convexe, alors nous obtenons le schéma de la paroi marginale d'un atoll soulevé ou encore celui d'une colline ou piton sous-marine soulevés, du lagon.

En aucun cas cette figure ne peut être le schéma d'un atoll entier.

Voici comment à mon avis l'on doit admettre la structure d'un atoll.

Je vais essayer de raccorder mon point de vue avec celui de Darwin. Pour cela, nous allons considérer, dès l'abord, que dans la fig. 6 (p. 152) les 2 points A″ A″ sont reliés par une horizontale qui sera sous le niveau de l'eau ou au-dessus selon que l'on aura à faire à un atoll vivant, actuel, ou à un atoll soulevé (île).

Le schéma ainsi constitué représentera la coupe de l'une des parois marginales d'un atoll, disons par exemple, celle sous le vent. Il nous faudra placer un autre schéma semblable plus à droite qui représentera la coupe de la paroi marginale au vent. Entre les deux schémas nous en placerons un certain nombre d'autres semblables ou plus étroits représentant les collines et pitons du lagon. Tous les vides intermédiaires sont remplis par du sable et les socles initiaux raccordés entre eux. C'est l'ensemble de ces vides qui constitue le lagon dont la portion supérieure seule n'est pas ensablée.

Si la ligne A″ A″ est à quelques mètres sous l'eau il existe en surface un récif actuel prospère; si cette ligne est au niveau de l'eau, ou au-dessus de l'eau, c'est que l'ensemble a été soulevé et nous avons à faire à une terre, à une île, et non plus à un récif. Le récif frangeant vivant s'est reformé sur la pente extérieure comme tout à fait au point de départ lorsque le récif s'est constitué sur la côte du socle initial avec la seule différence qu'il est ici comme "suspendu" sur la paroi, au lieu d'être basal.

- - - - - - - - - - -

SUMMARY

Darwin believed that the archipelago of Tuamotu consisted of present living atolls in which the process of subsidence was still going on

in our days. Dana shared this opinion, too; however, for him, Makatea and Niau, among others, constituted exceptions.

Couthouy and Agassiz first expressed the idea that all the islands of Tuamotu had undergone the effects of a relatively recent elevation. But, for them, the sequence of events which had affected these elevated atolls had not been correctly defined.

Considering that the elevated calcareous corals of Makatea are 80 meters high and that, as we know, corals do not live under 40-50 meter depths (a fact which I have confirmed at Hikueru), one must conclude, as Darwin did, that these enormous calcareous coral beds (known to be much thicker under water, according to recent depth-findings), could only have been formed in the course of a slow subsidence of the underlying base at the speed of coral growth. This process was interrupted by pauses and even by elevations.

The extremely irregular form and the varying general direction of the islands of Tuamotu lead to the conclusion, among others, that the general shape of the old atoll is not due to the action of prevailing winds, but primarily and fundamentally to the form of the original base, which can only be an island such as Darwin had imagined.

Yet, one must admit that, with respect to the details, several modifications must be applied to Darwin's scheme.

Here are the conclusions to which I have come after 8 months of research on the Tuamotu islands and of 10 years of studies on the coral and coral reef literature.

All the islands of Tuamotu have undergone a recent elevation, which I can date as belonging to the quaternary period, because the actual molluscs *Tridacna* and *Turbo* are consolidated with blocks of coral which are of the same species as those living today on the outer slope.

The consolidated *Tridacna* and *Turbo* are found on the summit of the cliff of Makatea as well as on the shallow fog flat of Hikueru, of Takume, of Fakarava, Takapoto, Takaroa, Apataki, Anaa, Rangiroa, Niau, etc.

We are, therefore, not dealing with different levels of erosion as Agassiz supposed, but with different levels of elevation: Makatea was elevated to 100 meters, Niau to 5, the others to 3 or 4 meters above sea-level.

Firstly, we must keep in mind one consequence of the fact that all the atolls were elevated . . . namely, that the shallow islands of Tuamotu are not reefs at all, nor actual living nor stationary atolls. They are lands, islands, quite simply. They are bases of calcareous fossil coral on whose submarine slopes there have developed new fringing reefs, actual and alive, as they developed at the beginning, on any base. It is absolutely erroneous to designate the different portions of the islands by the terms "slope of the reef," "reef flat," (also called "fringing reef" by Darwin and almost all the geologists after him), or "reef." We are in fact dealing, respectively, with the submarine slope of the base of the island, the coastal shelf by abrasion and the base of calcareous fossil coral which constitute the island.

We are not concerned solely with a modification of terms, but with something much more important. We are dealing with a different way of viewing the facts. The consequences are significant. One should not try, in a desperate attempt to "save," if I may say so, the term "reef" for the case under our study, to attribute to it the meaning of "shallow rock." It was not thus that Darwin had conceived it. He believed that his fringing reef and his barrier-reef were living things, active in our days.

- - - - - - - - - - -

Immediately after their emergence, the sea began to attack these shallow new lands, sculpturing them into cliffs. Makatea, however, represents a particular case that does not enter into the general picture. The sea abraded the zones of consolidated sediment rather rapidly; the consolidated coral blocks offered more resistance and were only gradually abraded, subsisting in our days in the form of islets.

At the beginning, the sea flung itself to the summit of these coral rocks and formed there a first beach with a dike (rampart) of pieces of worn coral.

But, directly after, at ebb-tide, level along the border of the island, at the level where the surf breaks, calcareous Lithothamnion algae started to build a formation which at present has a height of approximately 5 meters under water. The breakers beat this veritable living cliff which is pierced by innumerable tiny holes, against which they crash and spend themselves, and come to form the actual beach at a distance of a few to a hundred meters or more beyond the border-ledge, depending on local conditions.

At Makatea, and at Niau, the cliffs are spectacular, but in the shallow islands it took me a good deal of time to become aware of their existence. However, it was just this notion which permitted me to see certain phenomena more clearly.

This shallow cliff retreated steadily, leaving between itself and the original border a more or less wide flat produced by the abrasion of the marginal portion of the island at the level of low-water.

This is a coast flat such as the sea creates at the edges of all the continents which it attacks. Here, it is a mass of fossil coral that it destroys, completing in fact the work of living perforating organisms and of the "rodents" of stones. Boulders of all sizes joined to the substratum of which they are a part, just above the water, witnesses to the ancient level. They should not be confused with the rocks torn by the sea from the border and thrown back on the flat. The latter usually bear the sign of their origin: they have a thick bed of Lithothamnion algae. It is incorrect to call this formation a "reef flat," or even a "fringing reef," especially since this flat is frequently bleakly destitute of living corals.

Behind the cliff, beyond and below the dike proper, we have what may be called the "flat of sea fog," then, the subfossil dike, and, finally, the summit of the island.

Between the actual dike and the subfossil dike we find a difference in altitude of 1.50 (one and a half) meters. I do not believe that this is due to a variation of the sea level. If there were no Lithothamnion ridge nor coastal flat, the breakers would reach the summit, crashing at the old dike, as is the case in the village of Taheto at Takume. At Hikueru, in August, 1952, a large swell from the south completely moved back the entire dike of the present beach 4 or 5 meters further inland.

- - - - - - - - - - -

What constitutes the marginal portion of the islets which the sea abrades at present? The spray flat gives us the clues . . . . It is "a vast field of ruins. Angular masses of coral rock, varying in dimensions from one to a hundred cubic feet, lie piled together in the utmost confusion; and they are so blackened . . . . as to resemble the clinkers of Mauna Loa . . . . Such regions may be traversed by leaping from block to block, with the risk of falling into the many recesses among the huge masses . . . . Some of the blocks, measuring five or six feet in each of their dimensions, were portions of single individual corals; while others have the usual conglomerate character of the reef rock." —Dana, 1872.

This spray flat, blackened by the brown mucilage secreted by the *Algae Cyanophycées* which cover it and which are the "rodents" of limestone and other rocks, was slightly eroded at the beginning of the elevation, when the coastal flat was at its initial stage.

Thus, the picture before us, although a little aged and eroded, is still that of what was once a very prosperous reef, composed of voluminous individual corals pressed against each other, interlaced to such an extent that they had become more or less inextricable. It was enough for me to plunge in certain zones of the New Caledonian coast to understand this.

Today it is a mass of quaternary fossil coral blocks, in their initial place and slightly eroded. They are not at all drift matter, strewn at that point by the storms; if they were, their positions would be different. They are truly in their place.

- - - - - - - - - - -

The present living coral reef begins at the Lithothamnion ridge and extends down the outer slope, under the water, of the island, to depths of 40 meters approximately, as far as I could see.

This present coral reef is made up of relatively small individuals, more or less distant from each other. It is a poor thing compared to those which built the immense calcareous masses from the Cretacean to Miocene periods and left us their traces in the cliffs of Makatea. In our days, in Tuamotu the destructive forces are far more powerful than the constructive ones. But this will not always be so, perhaps.

The quaternary reef must have been 10 to 20 meters below sea level, for corals growing at less than a meter under water are not very voluminous; they are flattened, sometimes encrusting. Our observations also lead to the conclusion that the waters around Tuamotu must have been warmer.

- - - - - - - - - - -

In general, the coastal flat is eroded at 30 centimeters below ebb level. As far as corals are concerned, it is an immense desert. But, at times, as a result of fissures in the border of the Lithothamnion ridge, or as the result of a deeper abrasion in a zone of consolidated sediments, there may remain at ebb 80 centimeters to 1.5 meters of water. In this case, the corals "climb" the slope, so to speak, and grow in this particular zone. But they are only rare species represented by short, flat individuals, often encrusting and difficult to recognize.

In the lagoons without channels, the *Porites* grow in the largest numbers; in the lagoons with channels, numerous ramified Acropora prevail.

- - - - - - - - - - -

We have seen that the Lithothamnion ridge formed on the border of the coastal shelf produced by abrasion. It is very important that we note that this formation of calcareous algae develops best at the spots where the surf breaks, in ebb water. These algae never develop on living coral, but always on a dead fossil base. Now, since this base appears at the level of the water and is uncovered at low ebb, one is compelled to assume that it is there not as a result of stationing of the living coral, but through the effects of an elevation of the entire ancient base and its consequent abrasion.

The consequences of this statement are significant. All the Lithothamnion ridges are found on elevated fossil bases which are more or less abraded. What one calls barrier reef is nothing but an ancient fringing reef, elevated abraded. It must be pointed out that the difference between the "fringing reefs" and the "barrier reefs" of writers are very slight. Thus Davis says: "When a reef of the fringing kind fronts the open ocean it repeats the features of barrier reefs so closely that, except for the absence of a lagoon, its description may be taken from theirs, as given below." We know that certain portions of the "barrier reef of Tahiti" have a lagoon, others do not have any. In both cases, we are dealing with an ancient fringing reef which has been elevated and then abraded. Here again we have only one real present reef; it begins with the Lithothamnion ridge and develops on the outer slope of the ancient fringing reef, which was elevated, and now serves as its base.

- - - - - - - - - - -

If we examine the map of Plate I of Darwin's book "The Coral Reefs" in the light of these considerations, we come to the conclusion that all the blue portions represent only the coastal flats produced by abrasion in the elevated fossil atolls or the edges of fossil fringing reefs that were elevated and abraded. But in this last case, the blue line also represents the Lithothamnion ridge, which is the point of departure of the true fringing reef, alive and actual, which grows on the outer slope.

- - - - - - - - - - -

On the lagoon side there is also a coastal flat produced by abrasion, which is narrower and has a sandy beach. Then, rather abruptly, on the windward side of the islet, one reaches depths of twenty meters. The slope is less steep on the leeward side.

The Hikueru lagoon is no deeper than 38 meters at the center. This means that the slope is more or less steep down to 30 meters under water. Then there follows an immense central plateau measuring from 30 to 38 meters in depth.

From the bottom of white sand which covers all, submarine hills and peaks rise in great numbers.

They are built by fossil corals which have undergone, like the entire island, the quaternary elevation; the summits of many of them emerged above the water and were abraded. In places, there still remain witnesses to the ancient level. Some platforms, produced by abrasion, are as large as coastal islets, that is, they comprise 100 to 500 meters, and more.

Certainly, there occurred in the interior, on the slopes of the lagoon, deposits of huge coral blocks, brought by the sea from the coastal flat. But without a doubt, the submarine hills and peaks at the center of the lagoon have grown on a base which is far down in the depths. The cross-section of a lagoon hill is, in my opinion, exactly parallel to that of the ocean-border of the island, and I believe that its origin is the same.

In the lagoon, abrasion has only affected the emerging portions. One can observe, by the way, only one progressive filling process by the sand. Agassiz's theory, therefore, must be discarded.

- - - - - - - - - - -

The facts thus proved, however, lead us to make serious modifications in the Darwinian scheme. The fundamental phenomenon of subsidence, from all the evidence, does not permit the slightest modification.

But if we study Figure 5, p. 149, of the 1878, French edition of Darwin's "The Coral Reefs," we see that, on the line A′ C B′, Darwin has drawn coconut palms and a lagoon channel. This proves that we have before us a fringing reef, elevated and abraded; the channel is merely accidental, depending on the configuration of the original base. On Figure 6, p. 152, in A″ C′ A″, we have an image of an atoll with a central lagoon. This figure cannot be taken to represent the whole atoll. If we omit the concave upper line, the scheme only represents the cross-section of the marginal wall of an atoll or of a submarine hill in the lagoon: alive, if the upper line is above the sea level, and elevated if the line is drawn at sea level or below.

Here is how, in my opinion, one should envisage the structure of an atoll, combining Darwin's point of view and my own.

Let us place the scheme discussed above to the left, and a similar one to the right. Now we have the two walls at each extreme of an atoll. Between the two, let us place a certain number of other similar schemes, representing the submarine hills of the lagoon. Let us join the initial bases and imagine the intervening spaces which represent the lagoon, as being filled with sand up to a level of 40 to 100 meters beneath the present level of the sea.

The whole constitutes the scheme of an entire atoll, alive, if the upper surface is under the level of the sea and of an elevated atoll or island if the upper surface is above the level of the sea.

- - - - - - - - - - -

NATURE AND ORIGIN OF ATOLLS[1]
A PROGRESS REPORT

By Preston E. Cloud, Jr.
U. S. Geological Survey
Washington 25, D.C., U.S.A.

Introduction

Atolls (Darwin, 1837, p. 552) consist of ringlike organic reefs that surround lagoons in which there is no pre-existing land. The ring-reef, the lagoon, and the absence of pre-existing land are all essential features—even as small a remnant of the foundation rock as the siliceous volcanic pinnacle of Clipperton Island (Hertlein and Emerson, 1953, p. 349, pl. 26) disqualifies an otherwise perfectly atoll-like structure from admission to this elite class. Land, where present, includes only the low-lying, picturesque, "coral" islands that surmount the lagoonward margins of the peripheral outer reef and locally cap the larger patch reefs within the lagoon. Beneath the shady crown of tropic verdure that makes these islands habitable is but a thin cover of sand and gravel that rarely extends more than 20 feet or so above the reef-flat and is commonly only 8 to 12 feet high. This detrital veneer consists almost entirely of calcium carbonate of organic origin. Only bits of pumice from distant volcanic eruptions, and a thin layer of humus, relieve and enrich the gleaming whiteness of the "coral" strand.

It is, however, the reef beyond and beneath these evanescent islands that most excites the imagination of the geologist and the marine biologist. Since long before the days of Darwin, they have been arguing about how it got there, what it is made of, the organic community that lives on and in it, and what is likely to become of it in the future. Fortunately for the continued support of atoll research, this curiosity involves problems of consequence to anyone who is concerned with getting aboard or staying on an atoll island, with the carrying capacity of such an island for human habitation, and with the persistence or salvation of these features as habitable areas.

Happily also, atolls are of sufficient variety that it will be necessary to study many of them before the essential questions can be answered with reasonable assurance and permanence. Until now, atoll study has been seriously handicapped by the limitations of individual experience, interest, and opportunity—even Darwin actually examined at first hand only south Cocos-Keeling atoll and that not intensively (Wood-Jones, 1910, p. 216). Within the past four years, however, the Pacific Science Board, through its Atoll Research Program, and on the basis of committee recommendations, has deliberately selected atolls believed to typify broad structural and climatic types and sent to them research teams who have stimulated one another and minimized the danger of drawing generalizations based on too limited an approach. If this program is continued in the right directions, and to valid conclusions, it cannot help but greatly widen our sphere of understanding. On the other hand, the atolls studied to date are yet an inadequate sample of the variety known, and continuing subsurface studies and adjacent deep-sea surveys are needed, as well as surveys of the shoal-water surfaces of reefs.

---

[1] Publication authorized by the Director, U.S. Geological Survey.

The purpose of this symposium, as I understand it, is to summarize past and recently acquired knowledge and to synthesize views on the nature and origin of atolls as now comprehended. It is only in the sense of a progress report on the work of many present workers and their predecessors that the following attempt is made to survey the overall nature and probable origin of atolls.

Characteristics and Variety of Atolls

Atolls differ in location, size, association, shape, depth and growth-sedimentary pattern of the lagoons, nature of the reef-building community of organisms, features of the outer reef surface, structure of their foundations, age, history, and probably in origin.

Location *

Variations in the location of atolls are geographic, climatic, and in depth of the surrounding sea (Fig. 1). In the Atlantic we know only the aberrant bank atoll of Dry Tortugas, at the southwest end of the Florida Keys. Rocas Island, off the coast of Brazil appears to be an elevated atoll, with a lagoon only 2½ fathoms deep and a 65-foot high island (U.S.H.O. Chart No. 0537; Davis, 1928, p. 206). The Marquesas Islands, in the Florida Keys, are probably a ring-shaped dune cluster that only fortuitously resembles an atoll island-ring. Excepting Tortugas and Rocas no living atolls are known beyond the Indo-Pacific.

---

* Alexander Agassiz's excellent description of an apparently authentic Atlantic atoll, Hogsty Reef, in the Bahama Islands, at 70° 45'W. and 21°42'N. (1894, *Mus. Comp. Zool. Bull.*, vol. 26, no. 1, p. 103-108, pl. 2) came to my attention too late for inclusion in this discussion. From his account and profiles, Hogsty Reef appears to possess all of the features ordinarily attributed to oceanic atolls except reef islands. The annular wave-breaking reef of living corals and algae, 3 by 5 miles across, rises from water 900 to 1200 feet deep, and surrounds a lagoon 5½ fathoms deep."

and all but ten of these lie within the tropics. Within the tropical Indo-Pacific, however, atolls occur under conditions of both high and low rainfall, in areas of both appreciable and slight tidal variation and current strength, in the monsoon belts and beyond, in areas of both prevailing easterly and prevailing westerly winds, and rising from bottoms that range from thousands of fathoms to less than 300 fathoms deep (Sahul and Rowley shelves, N. W. Australia; see Fairbridge, 1953, esp. Fig. 2; also U.S.H.O. Chart No. 3420).

Of the 330 or so[2] known and probable atolls accounted for in Figure 1, well over half are included in the Tuamotus (62), eastern Indonesia (37), the Caroline (32) and Marshall (29) Islands proper, and Fiji (25)—named in the order of most numerous atolls. If to these are added the atolls of the Maldive (23) and Laccadive (11) Islands, the Gilbert (11) and Ellice (7) Islands, the Coral Sea area (14-18), the South China Sea (10–15 or more), the Bismarck-Solomon chain (11–13), and northwestern Australia (5–6), about four-fifths of all known atolls will be accounted for. The principal additions to those recorded by Darwin (1896, pl. 3) are in eastern Indonesia, resulting from the work of Umbgrove and Kuenen (Umbgrove, 1947); along the Australian shelves, for which Fairbridge (1950, esp. Fig. 10) has summarized the latest information; and in eastern Fiji, as noted by Ladd and Hoffmeister (1945, pp. 157–158, Fig. 2). In keeping with the general rarity of reef growth in the cool waters of the western coasts of continents, no atolls are found along the eastern Pacific coast.

Little is known of the 10 known and supposed modern atolls that lie outside the Indo-Pacific tropics. H. T. Stearns reports (1946, p. 94) that the principal lime-secreting organisms of Midway (28°N) and adjacent reefs are coralline algae. Middleton and Elizabeth reefs (30°S) are presumably south of the present limit of coral growth, and may be dead or formed of reef-builders other than corals. Minerva reefs, Saumarez Atoll, and Oeno and Ducie atolls are just south of the tropic of Capricorn and may be normal coral-algal reefs.

Size, association, and shape

The isolated individual ring-reefs, such as are commonly regarded as the typical atoll form, range from minute rings only a mile or two in diameter (Ifalik, Fig. 2, and others in the Carolines; Nukusongea and others in Fiji, Ladd and Hoffmeister, 1945, pp. 158–159) to the great ring-reef of Kwajalein (Fig. 2), which is 75 miles long and averages 15 miles wide. Other atolls are small satellites to larger reef-complexes like Kayangel (5 by 2.5 miles, see Fig. 2) and Ngaruangl, off the northern end of the Palau group, Kuop (12 by 5 miles) off southeastern Truk, and the many atolls of the great Fijian and eastern Indonesian reef-complexes.

---

[2] A check list by E. H. Bryan, Jr. (1953), received after completion of the present report, records "about 400." His list is extended by the inclusion of about 60 known table reefs which are mainly from the western Indian Ocean and the Admiralty, Caroline, Marshall, Gilbert, and Tuamotu islands, as well as by 26 bank areas in the Caribbean Sea. The deletion of these inadmissible lagoonless islands and banks is slightly compensated for by my inclusion as atolls of wave breaking ring-reefs without islands. This extends the southern range recognized by Bryan and increases the apparent atoll count for Fiji from 8 to 25.

I have also learned, since writing this, of two Red Sea atolls, Recif Vert and Sanganeb, which seem to resemble the typical oceanic form (Nesteroff, 1955, p. 38; Rathjens and Wissman, 1933, p. 115, 184).

In the Maldive Islands, most of the "atollons," from which the name atoll is derived, consist of ring-reefs within ring-reefs, and reach large sizes. Thus Ari Atoll is about 50 nautical miles long by 17 miles wide and the atoll-complex of Miladumadulu-Tiladumadulu at the north end of the Maldive group is about 80 nautical miles long by 18 miles wide; Suvadiva, a "simple" atoll at the south end of the group, is roughly 35 by 45 miles across. The lagoons of Maldive atolls range to 50 fathoms depth, with passes between atolls and parts of atolls well exceeding 100 fathoms (Darwin, 1896, pp. 45, 51–52; Fig. 3 of present paper). The small ring-reefs that make up the composite atoll rim, or rise within the lagoon, have been called faros, after the political subprovince of an atollon; and the faro lagoons attain depths of more than 12 fathoms (Darwin, 1896, p. 45). Not only are the faros arranged in large rings, however—the entire Maldive group is a gigantic ringlike double row of atolls 470 miles long and up to 65 miles wide. Both the small individual rings (some as large and deep as isolated atolls elsewhere) and the large composite ones were included as atolls by Darwin in the Beagle account (1845, p. 502), although he more cautiously referred to the faros as merely "ring-formed reefs" in his later book (1896, pp. 45–46).

With conspicuous exceptions, such as Namonuito (25 by 45 miles) in the Carolines, larger atolls seem most generally to characterize areas of probably long continuing subsidence away from high islands. Such are the atolls of the Tuamotus, Marshalls, and Maldives. Small atolls, on the other hand, seem to be commoner in areas associated with high islands and suggestions of fluctuating sea level, as in the Carolines, Fiji, and Indonesia. Alignment in northwest-southeast trending lines is characteristic of the arrangement of atolls in the open Pacific away from the Caroline swell (Tuamotu, Line, Tokelau, Ellice, Gilbert, and Marshall Islands). The Caroline atolls are partly in northwest trending lines and partly east-west trending lines. The Maldives and Laccadives are oriented in north-south trending lines. Australian atolls parallel the coast. Few other atolls show conspicuous linear orientation, and the significance of the submarine ridges indicated by some of the atoll alignments noted is yet uncertain.

The outer ring-reefs of many atolls approximate simple geometric shapes, such as circles, ellipses, triangles, and rectangles. Others are irregularly looped, some are nearly pinched off into several atolls, and some display hornlike projections that have separate shallow lagoons (Arno). Figure 2 illustrates a selection of well-known atolls of simple plan form for comparison of sizes, shapes, lagoons, and islands. Figure 3 shows the variation in pattern from simple to composite of the Maldive atolls.

Depth and nature of lagoons

Although Daly (1910, pp. 300–301) attempted to show that the average maximum depths of "representative atoll lagoons and barrier channels of the Pacific and Indian oceans . . . is about 35 fathoms," depths of atolls as recorded range from about 50 fathoms to very shoal. Ringgold Atoll in Fiji, for instance, is said (Daly, 1910, p. 301; Davis, 1928, p. 93) to reach a depth of 52 fathoms, and Davis (1928, p. 93) reports 49 fathoms in the lagoon of an atoll only three miles in diameter in the Solomons (Rura Sura, which I have not seen on charts). On the other hand, the maximum depth of the lagoon at Onotoa (Gilbert Is.) is only a little over 8 fathoms, Gardner Atoll (Phoenix Is.) has a sounding of less than 4 fathoms, Sydney (Phoenix Is.) has less than 4, and Washington Island (Line Is.) has a very shallow brackish pond instead of a lagoon. The lagoon at Cocos-Keeling is also very shoal. Atolls may thus grade to table reefs with emergence or filling of the lagoon (Cloud, 1952, Fig. 4), though table reefs do not necessarily pass through an atoll stage. The atoll lagoon likewise varies in respect to proportionate area of the atoll included, general topography of its bottom, and frequency and size of patch reefs, as well as other patterns of organic growth and sedimentation.

Perhaps one of the most aberrant lagoons is that of Christmas Island (Fig. 4) in the Line Group—the atoll with the largest land area. Here the small lagoon is restricted to the wide northwestern end, is everywhere shallower than 4 fathoms, and may be nearly filled with sediment. The narrower southeastern end has numerous ponds that may represent lagoon remnants, and the intervening land locally reaches an elevation of 35 feet. Palmyra Atoll (Line Is.) also has an unusual lagoon, accounting for well under half of the total atoll area, and divided into 3 small parts by a reef bridge and a shoal area (Fig. 4). Each part, however, reaches depths greater than 25 fathoms. The atolls of the southern Gilbert Islands (*e.g.*, Onotoa, Fig. 2) hardly have lagoons in the conventional sense—only broad western banks with slightly shallower reef rims and low thresholds in the passes to the open sea. Elizabeth and

Middleton reefs likewise are borderline cases, as is Rocas Island. The shallower, smaller lagoons in general seem to have more patch reefs per unit area than the deeper and larger ones—probably because they afford a proportionally greater area within the depth range of vigorous reef growth and are more rapidly flushed and thus better oxygenated.

Nature of the reef building community of organisms

Although atolls and other organic reefs are ordinarily included under the broad heading of "coral" reefs, a wide variety of organisms contribute to the construction of the reef-frame or deposit their hard parts within it. In addition to the conventional reef-building corals or Scleractinia, the alcyonarian *Heliopora* is an important and locally (Onotoa, Funafuti) a dominating frame builder. The hydrozoan *Millepora* also at places (*e.g.*, Cocos-Keeling, Butaritari, Maldives) contributes significantly to the framework of the reef as emphasized by Darwin (1896, pp. 9–11, 46; Wood-Jones, 1910, p. 133; and Gardiner, 1931, pp. 89, 171). The importance of the coralline algae in binding and building the frame is hard to overrate, although it has been done (Finckh, 1904, p. 147; Setchell, 1928, pp. 1841, 1843). Crustose coralline algae are known to be the principal or sole builders of some reef units and important associates of corals in most post-Paleozoic reef building. H. T. Stearns (1946, p. 94) reports barnacles as accessory contributors to the present reef at Midway, and they are known to form thick, upright, potentially reeflike clusters in clastic Tertiary sediments of California (Woodring, *et al.*, 1940, p. 96, pl. 27A). Many other types of organisms also contribute to the reef mass in one way or another—either as accessory frame builders or binders (Cloud, 1952, pp. 2133–2144), as surface veneers, or by providing clastic particles that wash into the interstices of the cavernous frame and help to fill it up and create a potential rock mass.

The entire outer structure, up to the highest point that is wetted by the daily tides, teems with a great variety of plant and animal life. On close examination it seems as though some living thing crawls on, bores into, hides in natural crevices and crannies of, or clings to every inch of the reef—each feeding on and being preyed upon by something else. Still other hosts of organisms live on or within forms larger than themselves, while over and around the whole the freely swimming predators and algal browsers take their daily toll or become a morsel of food in the complex chain.

Features of the reef surface

The surface of the ringlike outer reef may be one of luxuriant growth of reef-building organisms, or it may be an erosionally truncated and seemingly barren area inhabited only by a thin film of algae and crevice-dwelling or tide pool organisms. This depends on whether it has recently been exposed to subaerial or intertidal effects, the extent and length of such exposure, and the onset of subsequent resubmergence.

All reef surfaces, regardless of other factors, tend to display zones of organic growth, detrital construction, and erosion. These appear to be either parallel to the reef front, but random within zones, or to consist of features that individually are normal to the reef front but are also arranged in parallel zones. The former patterns are said to be concentric and the latter radial. The genetic significance of these patterns if any is yet uncertain, but the observed effects of known hydraulic erosion on limestone and rubble shores suggest that radial patterns are commonly erosional or inherited erosional, or represent a balanced erosional-constructional origin. Concentric patterns, on the other hand, seem to be mainly constructional and environmentally controlled, but may be in part erosional or inherited erosional. The larger reef islands that parallel the reef margin are thought to be mainly constructional-concentric. Their presence at the inboard margin of a reef flat impedes the flow of water over the reef, accentuates return current flow seaward, and probably affects the development of radial patterns such as the comb-tooth groove and spur systems that extend seaward through the peripheral algal ridge of parts of many reefs.

Although most atoll reefs are at some places capped by peripheral islands but lack lagoon islands, some atolls are simple ring-reefs with no islands at all (Minerva reefs, some east Fiji reefs) and others (*e.g.*, Maldive atolls, Green or Nissan Atoll) have sand islands of fragmental calcium-carbonate on patch reefs in the lagoon, as well as on the outer ring-reef.

Structure, age, and history

The outer or peripheral ring-reef is the most essential part of an atoll but only a small part of its total bulk. This growing linear reef ridge encircles a lagoon that is the site of accumulation of calcium-carbonate sand, silt, and gravel of organic origin, and that contains varying numbers of individual, irregularly-shaped patch reefs (Cloud, 1952, Fig. 3). The outer reef slope is veneered and extended seaward by rubble from normal attrition and slumping. Borings near atoll margins have shown that the three-dimensional result is complex, varied, and mainly clastic. The fossil biota consists almost exclusively of lagoon- and reef-dwelling, shallow-water forms (Hinde, 1904; Grimsdale, 1952; Ladd, *et al.*, 1953) with rare occurrences of deeper water forms of the outer reef slope, such as *Cycloclypeus* (Grimsdale, 1952). This suggests the fairly continuous presence, but not the continuous upward growth, of a peripheral ring-reef.

The overall structure, age, and history is related to constructional and erosional processes and depth relations that determine when, where, and how, suitable foundations are provided for growth of ring-reefs; to crustal subsidence, rise of sea level, or upward growth that results in evolution of the atoll form; and to later changes of sea level, oxygen and nutrient supply, temperature, insolation, wind direction, and hydraulic factors such as affect continued growth, decline, and rejuvenation of the vital reef ring.

Volcanism, sedimentation, fall or rise of sea level, and tectonic uplift or subsidence may provide platforms on which reefs can grow. With effective subsidence, due either to crustal depression or rise of sea level, or under proper conditions of growth without subsidence, an atoll might evolve from such a reef. With time it would come under the shaping influences of wind, tide, and current, and would vary further in structure according to the organisms of which it was constructed, their biologic associations, rate of sedimentation in the lagoon and on the outer reef slope, and the strength and rigidity of the total mass. Hydraulic wedging in the surf zone, slumping of weakly supported outgrowing organic masses, and sea-slides would affect individual reefs according to their organic make-up, their location with respect to storm paths and seismic belts, and their rate of upgrowth and consolidation.

Pleistocene and Recent world-wide fluctuations of sea level, due to growth and decline of glacial ice, and consequent change in volume of ocean water, introduce a final variable. Atolls and other reefs were differently affected according to their proximity to sea level at the time of each fluctuation, and according to local movements of the earth's crust. Some were probably "drowned" (*e.g.*, Chagos Archipelago, Fig. 5; bank east of Ulithi) by being carried below depths at which the reef-association could survive; while associated reefs were able to maintain their position near sea level by continued upgrowth or were fortuitously submerged to just the right depth for present reef growth. Others were exposed to the atmosphere and planed off or otherwise modified by subaerial and intertidal solution and abrasion, like Maratoea and Kakaban, east of Borneo (Kuenen, 1947; 1950, pp. 437–438, 469–470). Still others were brought into zones of more vigorous organic growth.

That widespread death of reefs occurred during Pleistocene time through chilling or "asphyxiation" by suspended "mud," as suggested by Daly (1910, 1948), is rendered unlikely by the occurrence of probable late Pleistocene coral-algal reefs as far north as 15° in the Mariana Islands (carbon 14 date by J. L. Kulp). However, the principal element of Daly's glacial control hypothesis remains valid—eustatic oscillations of sea level during the Pleistocene. If to this we add Recent changes of sea level as well, we have probably the most important controlling factor in the general morphology, history, and superficial aspects of those parts of modern atolls and other organic reefs that rise above the 50-fathom line. The time at which reef growth began on any given atoll foundation, and its subsequent history, can be determined only by correct interpretation and geologic dating of appropriate subsurface samples.

ORIGIN OF ATOLLS

To account for all of the different patterns, structures, and associations of atolls is the proper but difficult objective of any hypothesis of atoll origin. Only modern atolls will be considered at this place, on the assumption that if the atolls of the present sea can be explained it will be fair to consider that broadly similar mechanisms may be evoked to explain the atolls of the past. The principal conclusion from the present review is the now highly unoriginal one that no single simple theory of atoll origin in the terms originally proposed is adequate to account for all known atolls. Rather, that which withstands critical review in each of them has evolved almost imperceptibly through the efforts and writings of many into a modern synthetic hypothesis of complex origin. This owes its most important parts to Chamisso, Darwin, and Daly, and some of its most telling recent facts to Ladd and Kuenen, but it is properly attributable to no individual.

The name of Charles Darwin inevitably and properly comes to mind whenever atoll origin is considered, for he was the founder of the important and durable subsidence hypothesis of reef evolution, which sought primarily to explain the atoll form. Although first read before the Geological Society of London on May 31, 1837, and later the subject of a book (Darwin, 1889), the best known account of this theory is probably that given in the "Voyage of the Beagle" (Darwin, 1845, pp. 501–518, diary entry for April 12, 1836).

Darwin here (1845, p. 502) tells how "the earlier voyagers fancied that the coral-building animals instinctively built up their great circles to afford themselves protection in the inner parts," how a then prevailing theory apparently originated by Lyell (F. Darwin, 1898, p. 293) invoked growth on the rims of submarine craters as the basis for the atoll form, and how Chamisso "thought that from the corals growing more vigorously where exposed to the open sea . . . the outer edges would grow up from the general foundation before any other part, and that this would account for the ring or cup-shaped structure." He then unfolds his own interpretation whereby fringing reefs change to barriers, and barriers to atolls, with progressive slow subsidence of the ocean floor beneath. "If," Darwin (1845, p. 504) asserts, "the foundations, whence the atoll-building corals sprang, were not formed of sediment, and if they were not lifted up to the required level, they must have subsided into it; and this at once solves the difficulty . . . I venture to defy anyone," he continues, "to explain in any other manner, how it is possible that numerous islands should be distributed throughout vast areas—all the islands being low—all built of corals, absolutely requiring a foundation within a limited depth from the surface."

The broad elements of Darwin's theory are attractive in their simplicity and one needs but to examine the chart of a reef tract such as the Fiji Islands (Fig. 6) to be impressed by the seemingly gradational forms between the several principal reef types. But the apparently simple may be deceiving, and some of the most vigorous objections to the subsidence hypothesis have been based on studies of the Fiji reefs.

Darwin himself did not consider that the evolution of atolls was entirely a matter of continuing gradual subsidence. In his presentation of the subsidence theory, he (Darwin, 1845, pp. 501–518) emphasized the importance of pre-existing foundations at originally slight depth, and he realized that reefs *could* grow to the surface from such slight depths without subsidence. But he did not suspect the influence of fluctuating sea level, and, in particular, that due to Pleistocene glacial control.

In a series of papers, extending from 1910 to 1948, R. A. Daly later provided the missing ingredient. Until very recently the tendency has been to regard glacial control and crustal subsidence as alternative rather than complementary hypotheses, and evidence for and against subsidence in the Darwinian sense has continued to be found and discussed. Despite the force of the paleontologic data from mid-Pacific seamounts (Hamilton, 1953) and of the drilling and marine geology studies summarized by Shepard (1948, pp. 669–670) and Kuenen (1950, pp. 445–458, 477) there seems still to have been some lingering doubt as to the degree and significance of subsidence. The essential fact of great subsidence of atoll foundations, however, was finally established once and for all, by the most direct method, when a U. S. Navy project under the direction of H. S. Ladd (Ladd, 1952; Ladd, *et al.*, 1953) drilled a hole to basalt at 4170 feet beneath shallow-water early Tertiary sediments under Eniwetok Atoll. The last retreat for those who would discount the importance of subsidence in reef evolution is now the contention that great subsidence has not been incontrovertibly demonstrated in all areas where modern atolls occur, that some reefs grow even under conditions of emergence, and that atolls are very rare in or absent from areas of presumed subsidence in the tropical Atlantic—a mystery still.

On the other hand, while crustal subsidence may well be responsible for the location and general outline of most present atoll foundations, it is now apparent that the original Darwinian hypothesis of atoll origin was oversimplified and requires modification and elaboration. It appears that there are at least three plausible ways in which the atoll form might originate and persist: (1) slow crustal subsidence beneath a barrier reef or a fringing reef, or beneath a bank or a rimmed structure (erosional or constructional) on which a ring-shaped reef might grow; (2) slow eustatic rise of sea level, around one of the same four kinds of structures; and (3) upward reef growth around the margins of a bank or a rimmed structure from depths not greater than 50 fathoms and probably not greater than 25 fathoms.

The first is basically Darwin's subsidence hypothesis, the second emphasizes the principal feature of Daly's glacial-control hypothesis, and the third is an outgrowth of Chamisso's views with adaptations to data on depth control and to take account of all the ways in which either flat or basin-shaped antecedent platforms might originate. The formation of a reef rim and linear reef growth, as suggested by Chamisso, would presumably be favored at bank margins, as soon as they were built or elevated to a wave breaking position, as a result both of accelerated oxygenation and precipitation of calcium carbonate through loss of carbon dioxide. These factors, however, would seemingly be effective only in water shallower than about 4 to 5 fathoms (Dietz and Menard, 1951, p. 2011), and could presumably affect the structure of atolls with deeper lagoons only in combination with subsidence, rise of sea level, or through superficial encrustation of pre-existing rimmed structures.

It is also of interest, in considering the three principal alternatives mentioned, to recall that maximum glacial lowering of sea level is generally believed to have been not more than about 50 fathoms below the present surface of the sea (*e.g.*, Flint, 1948), and to note the rarity or absence of atolls that rise from sea bottoms as shallow as 50 fathoms. At first thought this would appear to rule out both upward growth from antecedent platforms, and glacial control, as primary factors in the origin of atolls; while, at the same time, evidence from deep drilling shows that some, and probably many, atoll foundations have subsided conspicuously. On the other hand, and although it is probable that many modern reefs have Tertiary roots, it remains to be proved that a single Pleistocene or Recent reef anywhere grew upward continuously from a Tertiary reef as a base and without interspersed intervals of emergence caused by temporary downward fluctuations of sea level. Moreover, many atolls occupy only parts of broad submarine banks or ridges, and the great rarity of atoll lagoons more than 50 fathoms deep is a point in favor of their surrounding reefs having grown upward from antecedent high parts of such banks or ridges.

A supplementary explanation for the origin of atoll shapes by F. S. MacNeil (published 1954) is here summarized with his kind permission. He maintains that the shape of atolls is due to organic encrustation of basinal solution forms developed on table reefs or other limestone masses during a preceding period of emergence. From a comparison of reef morphology with limestone solution forms on Okinawa and elsewhere MacNeil concludes (1) that the annular reef is growing along a marginal solution rim, (2) that patch reefs in the lagoon are growing upward from residual pinnacles, and (3) that the linear reefs along the sides of deep channels are growing along the crest of limestone stream "levees" such as are well-developed on Okinawa. He explains faros by smaller scale emergence and resubmergence of pre-existing atolls. An example of a potential atoll foundation that may owe its annular form to subaerial solution, but which did not subside quite far enough to be crusted over by reef growth, is the Pelsart ring of islands in Houtman's Abrolhos (Teichert, 1947). The measure to which MacNeil's explanation of atoll morphology actually obtains will probably never be known, but it certainly applies in some degree and deserves incorporation in the general body of reef theory.

Available evidence and current thought thus suggests that although some and perhaps most of their basic foundations have undergone deep subsidence, many or most living atoll reefs may actually have grown upward from degradational antecedent platforms. The platforms are believed to have resulted from subaerial and intertidal erosion during and following Pleistocene sea level lowering; the upgrowth was concurrently with or following eustatic submergence introduced by melting glaciers. It is even conceivable (note Clipperton Island) that some atolls *may* have grown upward from the rims of undersea or submerged volcanoes, as was once believed to be generally true; though it seems most unlikely that this could be a common method of origin.

The three principal methods of atoll development suggested above may now be combined into a single hypothesis of complex origin that departs from the subsidence theory as promulgated by Darwin mainly in the recognition of glacial control and static upgrowth as important factors. Interplay of the three ways of producing or simulating subsidence, on a variety of foundation forms and materials, over different periods of time, and with varying secondary effects could probably produce a variety of atoll form and structure as complicated as that so far recorded.

A Recent 6-foot fall of sea level, which began perhaps 3,000 (±1,500) years ago, has widely affected the superficial aspects of atoll reefs. By exposing surfaces that lay near sea level before it occurred, it also provided foundations for the construction of many of the low reef islands that now occur on the atolls of the open Pacific and elsewhere, and via which the Polynesians were able to sail within striking distance of Hawaii.

In the final analysis atolls and atoll groups still present many individual problems, and we cannot yet be sure what the effects are in detail of the three supposedly principal factors involved in atoll origin. We may understand this and other elements of the reef problem better when: (1) more holes have been bored to atoll foundations, especially if directional holes can be oriented so as to follow and continuously core the area of maximum probability for most nearly continuous reef structure; (2) when comprehensive modern studies have been made of a composite atoll (Maldives), of a "drowned" or deeply submerged atoll or rimmed bank (Chagos, Ulithi), of some satellite atolls (Kayangel, Kuop) and atoll reefs without islands (Minerva reefs), of atolls with fresh and brackish water lagoons (Swains, Sydney), of a few table reefs (Washington, Phoenix, Enderbury) and atolls approaching the appearance of table reefs (Gardner), of the possible Atlantic atoll of Rocas Island, of Caribbean banks that might expectably support atolls, and of atoll-like Clipperton Island; and (3) when the entire reef tracts, and especially the atolls, of the shelf seas of Australia, of Indonesia, of the South China Sea, and of the Philippines have been made more fully known.

Bibliography

Bryan, E. H., Jr. Check list of atolls. Pac. Sci. Bd., *Atoll Res. Bull.*, no. 19, pp. 1-38 (1953).

Cloud, P. E., Jr. Facies relationships of organic reefs. *Amer. Assoc. Petr. Geol., Bull.*, vol. 36, no. 11, pp. 2125-2149, figs. 1-4 (1952).

Daly, R. A. Pleistocene glaciation and the coral reef problem. *Amer. Jour. Sci.*, vol. 30, pp. 297-308 (1910).

————. Coral reefs—a review. *Amer. Jour. Sci.*, vol. 246, pp. 193-207 (1948).

Darwin, Charles. On certain areas of elevation and subsidence in the Pacific and Indian oceans, as deduced from the study of coral formations. *Geol. Soc. London, Proc.*, vol. 2, no. 51, pp. 552-554 (1837).

DARWIN, CHARLES. Journal of researches during the voyage of H. M. S. Beagle. Undated recent reprinting by T. Nelson & Sons, Ltd., London. 543 pp. (original 1845).

————. The structure and distribution of coral reefs. 3d ed., Smith, Elder & Co., London, 344 pp. (1896, 1st ed. 1889).

DARWIN, FRANCIS. The life and letters of Charles Darwin, vol. 1. D. Appleton & Co., New York. 558 pp. (1898).

DAVIS, W. M. The coral-reef problem. *Amer. Geog. Soc., Spec. Pub.* no. 9: 596 pp., New York (1928).

DIETZ, R. S. and H. W. MENARD. Origin of abrupt change in slope at continental shelf margin. *Amer. Assoc. Petr. Geol., Bull.*, vol. 35, no. 9, pp. 1994-2016, figs. 1-12, pl. 1 (1951).

FAIRBRIDGE, R. W. Recent and Pleistocene coral reefs of Australia. *Journ. Geol.*, vol. 58, no. 4, pp. 330-401, figs. 1-12 (1950).

————. The Sahul Shelf, northern Australia; its structure and geological relationships. *Royal Soc. W. Australia Journ.*, vol. 37, pp. 1-33, map, figs. 1-8 (1953).

FINCKH, A. E. Biology of the reef-forming organisms at Funafuti Atoll. *Royal Soc. London, Rept. of Coral Reef Comm.*, The Atoll of Funafuti, Sec. 6, pp. 125-150, fig. 19 (1904).

FLINT, R. F., in Longwell, Knopf, and Flint, "Physical geology," 3d ed., John Wiley & Sons, Inc., New York, p. 195 (1948).

GARDINER, J. STANLEY. Coral reefs and atolls. MacMillan & Co., London, 181 pp. (1931).

GRIMSDALE, T. F. *Cycloclypeus* (Foraminifera) in the Funafuti boring, and its geological significance. *The Challenger Soc., Occasional Papers*, no. 2: 11 pp., text figs. 1-3 (1952).

HAMILTON, E. L. Upper Cretaceous, Tertiary, and Recent planktonic Foraminifera from mid-Pacific flat-topped seamounts. *Journ. Paleont.*, vol. 27, no. 2, pp. 204-237, figs. 1-5, pls. 29-32 (1953).

HERTLEIN, L. G. and W. K. EMERSON. Mollusks from Clipperton Island. San Diego Soc. Natl. Hist., vol. 11, no. 13, pp. 345-364, pls. 26-27 (1953).

HINDE, G. J. Report on the materials from the borings at the Funafuti Atoll. *Royal Soc. London, Rept. of Coral Reef Comm.*, The Atoll of Funafuti, Sec. 11, pp. 186-361, figs. 21-22 (1904).

KUENEN, PH. H. The borings on Maratoea and the coral reef theory of glacially controlled subsidence. *Kon. Ned. Akad. Wetenschap. Afd. Natuurk., Verh.*, Tweede Sectie, Deel 43, no. 3, pp. 1-35, figs. 1-14, pls. 1-3 (1947).

————. Marine geology. John Wiley & Sons, Inc., New York, 568 pp. (1950).

LADD, H. S. Recent reefs. *Amer. Assoc. Petr. Geol. Bull.*, vol. 34, no. 2, pp. 203-214, figs. 1-8 (1950).

————. Foundation of Eniwetok Atoll. *Geol. Soc. Amer., Bull.*, vol. 63, no. 12, pt. 2, p. 1273 (1952).

LADD, H. S. and J. E. HOFFMEISTER. Geology of Lau, Fiji. *B. P. Bishop Mus., Bull.* 181, 399 pp. (1945).

LADD, H. S., EARL INGERSON, R. C. TOWNSEND, MARTIN RUSSELL, and H. K. STEPHENSON. Drilling on Eniwetok Atoll, Marshall Islands. *Amer.*

Assoc. Petr. Geol., Bull., vol. 37, no. 10, pp. 2257-2280, figs. 1-5, pls. 1-2 (1953).

MACNEIL, F. S. The shapes of atolls: an inheritance from subaerial erosion forms. *American Jour. Sci.*, vol. 252, no. 7, pp. 402-427, figs. (1953).

NESTEROFF, W. D. Les récifs coralliens du banc Farsan Nord (Mer Rouge). *Ann. Inst. Océanogr., Résultats Sci. des Campagnes Calypso*, tome 30, pp. 1-53, figs. 1-11, pls. 1-21 (1955).

RATHJENS, KARL and HERMANN VON WISSMAN. Morphologische Probleme im Graben des Roten Meeres. *Petterman's Mitteilungen*, 79 Jahrg., pp. 113-117, 183-187 (1933).

SETCHELL, W. A. A botanical view of coral reefs, especially of those of the Indo-Pacific region. *Third Pan-Pac. Cong., Proc.*, vol. 2, pp. 1837-1843 (1928).

SHEPARD, F. P. Evidence of world-wide submergence. *Journ. Marine Res.*, vol. 7, no. 3, pp. 661-678, figs. 1-6 (1948).

STEARNS, H. T. Geology of the Hawaiian Islands. *Hawaii Div. Hydrography, Bull.*, no. 8, 106 pp. (1946).

TEICHERT, CURT. Contributions to the geology of Houtman's Abrolhos, Western Australia. *Linnean Soc. New South Wales, Proc.*, vol 71, pts. 3-4, pp. 145-196, figs. 1-7, pls. 6-16 (1947).

UMBGROVE, J. H. F. Coral reefs of the East Indies. *Geol. Soc. Amer., Bull.*, vol. 58, pp. 729-778, figs. 1-24, pls. 1-7 (1947).

WOOD-JONES, F. Coral and Atolls. Lovell Reeve & Co., Ltd., London, 392 pp. (1910).

WOODRING, W. P., RALPH STEWART, and R. W. RICHARDS. Geology of the Kettleman Hills Oil Field, California. *U.S. Geol. Survey Prof. Paper* 195, 170 pp. (1940).

ILLUSTRATIONS

FIG. 1.—Distribution of known and reported atolls.

FIG. 2.—Selected atolls compared at uniform scale.

FIG. 3.—Atolls of the northern Maldives.

FIG. 4.—Christmas and Palmyra Atolls.

FIG. 5.—Chagos Archipelago, showing atolls and submerged rimmed banks.

FIG. 6.—Portion of eastern Fiji reef-tract, showing apparent intergradation of reef types.

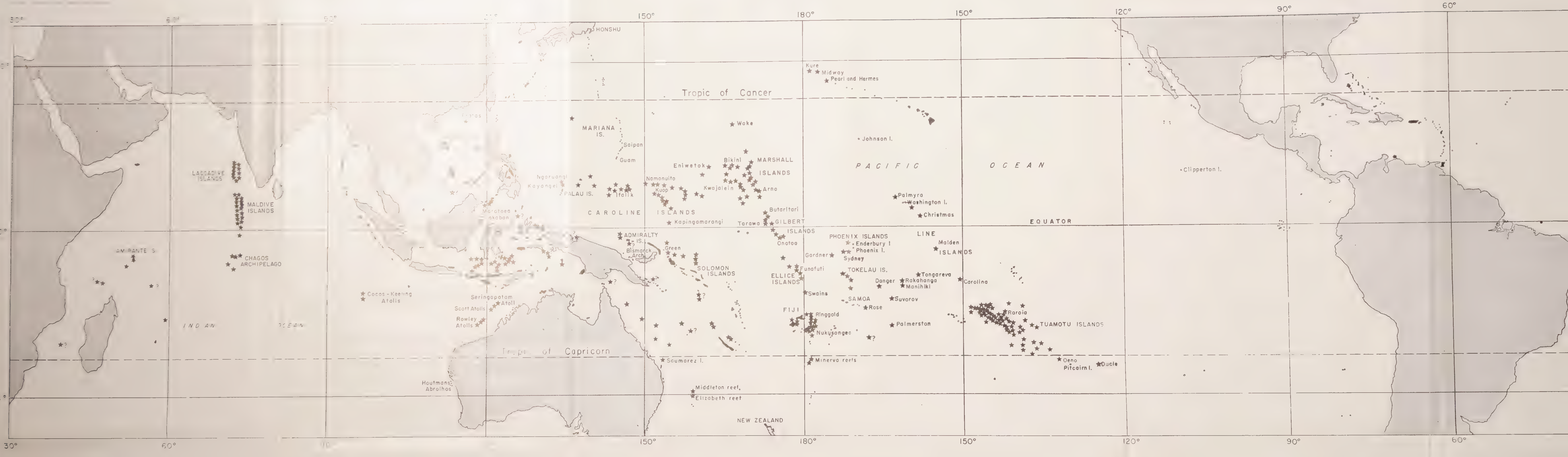

30°
60°
90°
120°
150°
180°
150°
120°
90°
60°
30°
0°
30°
HONSHU
Tropic of Cancer
Tropic of Capricorn
EQUATOR
Kure
Midway
Pearl and Hermes
Wake
Johnson I.
MARIANA IS.
Saipan
Guam
Eniwetok
Bikini
MARSHALL ISLANDS
Kwajalein
Arno
Namonuito
Kuop
Ngoruangl
Kayangel
PALAU IS.
Ifalik
CAROLINE ISLANDS
Kapingamarangi
Butaritari
Tarawa
GILBERT ISLANDS
Onotoa
PACIFIC OCEAN
Palmyra
Washington I.
Christmas
LINE ISLANDS
Malden
PHOENIX ISLANDS
Enderbury I.
Phoenix I.
Gardner
Sydney
Clipperton I.
ADMIRALTY IS.
Bismarck Arch.
Green
SOLOMON ISLANDS
Funafuti
ELLICE ISLANDS
TOKELAU IS.
Danger
Rakahanga
Manihiki
Tongareva
Caroline
Swains
SAMOA
Rose
Suvorov
FIJI
Ringgold
Nukusongea
Palmerston
Raroia
TUAMOTU ISLANDS
Oeno
Pitcairn I.
Ducie
Minerva reefs
Saumarez I.
Middleton reef
Elizabeth reef
NEW ZEALAND
LACCADIVE ISLANDS
MALDIVE ISLANDS
CHAGOS ARCHIPELAGO
AMIRANTE S.
INDIAN OCEAN
Cocos - Keeling Atolls
Seringapatam Atoll
Scott Atolls
Rowley Atolls
Houtmans Abrolhos
?

FIGURE I. - DISTRIBUTION OF KNOWN AND REPORTED ATOLLS

(⋆ indicates atoll or atoll cluster, uncertainly indicated by query)

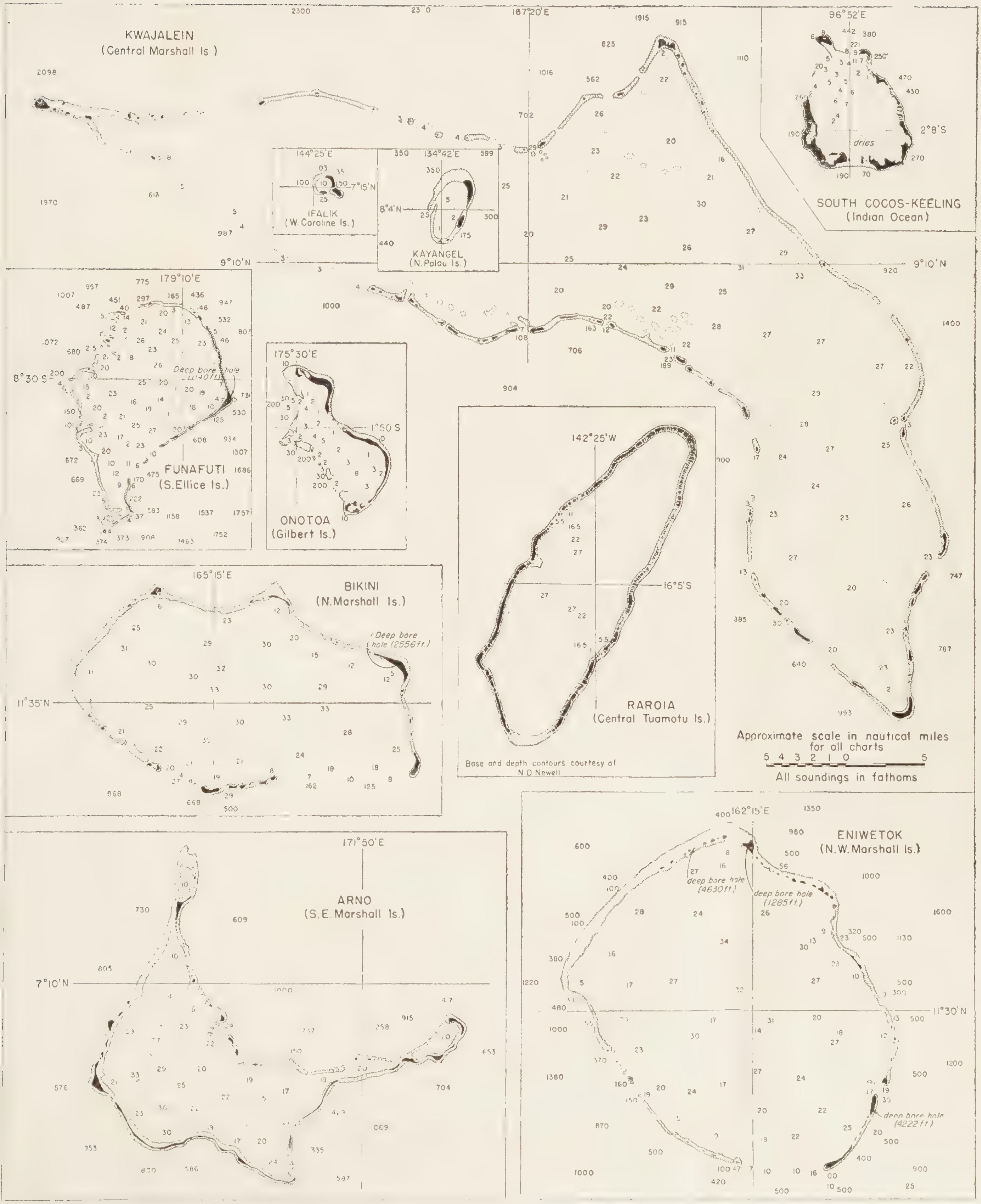

KWAJALEIN
(Central Marshall Is.)
167°20'E
96°52'E
dries
2°8'S
SOUTH COCOS-KEELING
(Indian Ocean)
144°25'E
7°15'N
IFALIK
(W. Caroline Is.)
134°42'E
8°4'N
KAYANGEL
(N. Palau Is.)
9°10'N
179°10'E
8°30'S
Deep bore hole (1140 ft.)
FUNAFUTI
(S. Ellice Is.)
175°30'E
1°50'S
ONOTOA
(Gilbert Is.)
142°25'W
16°5'S
RAROIA
(Central Tuamotu Is.)
Base and depth contours courtesy of N.D. Newell
Approximate scale in nautical miles for all charts
5 4 3 2 1 0 5
All soundings in fathoms
165°15'E
BIKINI
(N. Marshall Is.)
Deep bore hole (2556 ft.)
11°35'N
171°50'E
ARNO
(S.E. Marshall Is.)
7°10'N
162°15'E
ENIWETOK
(N.W. Marshall Is.)
deep bore hole (4630 ft.)
deep bore hole (1285 ft.)
11°30'N
deep bore hole (4222 ft.)

Figure 2. SELECTED ATOLLS COMPARED AT UNIFORM SCALE
(compiled from published charts except as noted)

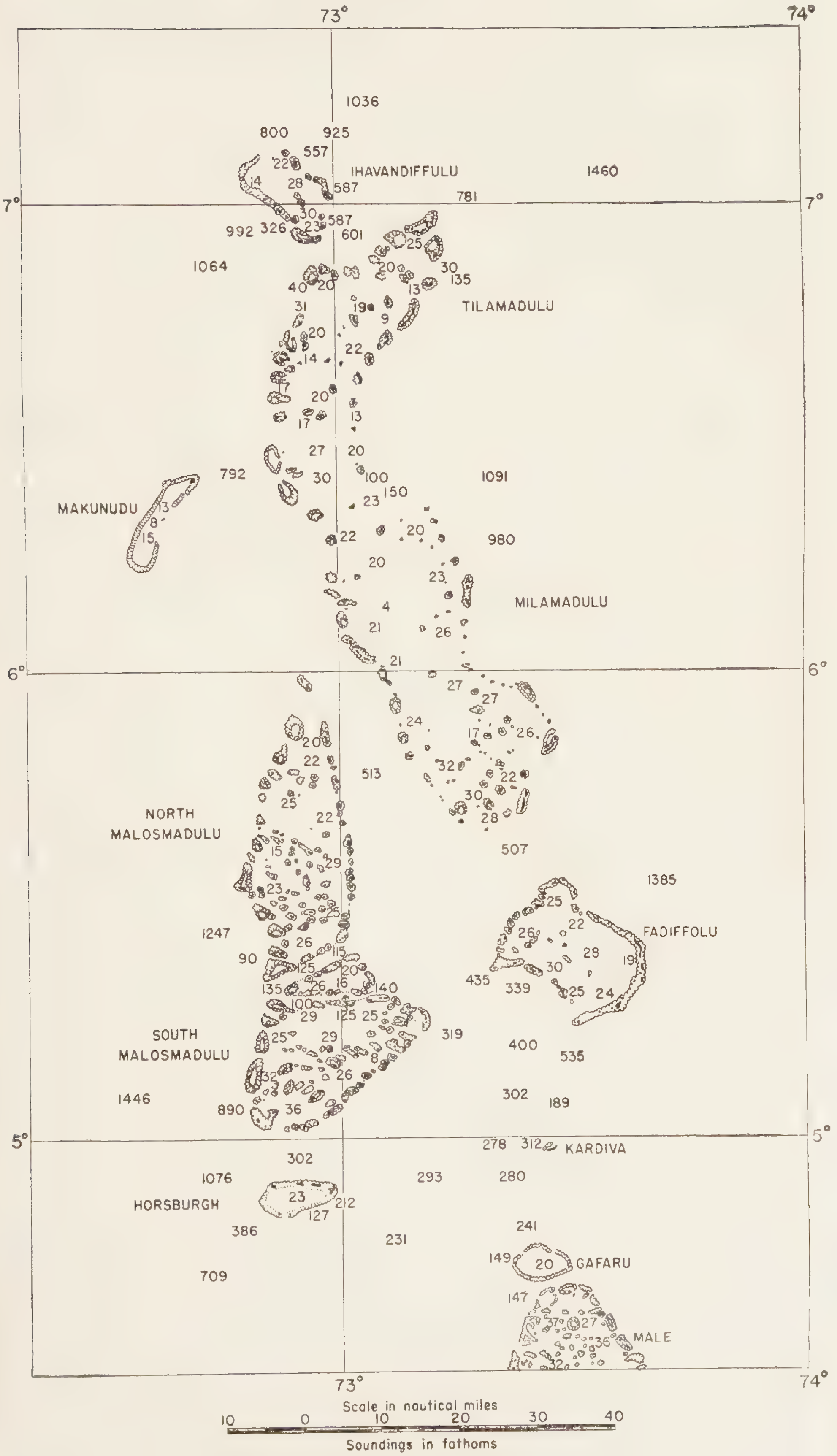

73°
74°
7°
6°
5°
IHAVANDIFFULU
TILAMADULU
MAKUNUDU
MILAMADULU
NORTH MALOSMADULU
SOUTH MALOSMADULU
FADIFFOLU
KARDIVA
HORSBURGH
GAFARU
MALE
1036
800
925
557
587
1460
781
992
326
601
1064
135
792
1091
980
513
507
1385
1247
90
435
339
140
319
400
535
1446
890
302
189
278
312
1076
293
280
212
127
386
231
241
149
709
147
Scale in nautical miles
10
0
10
20
30
40
Soundings in fathoms

Figure 3. Atolls of the northern Maldives
(after U.S.H.O. Chart No.1591)

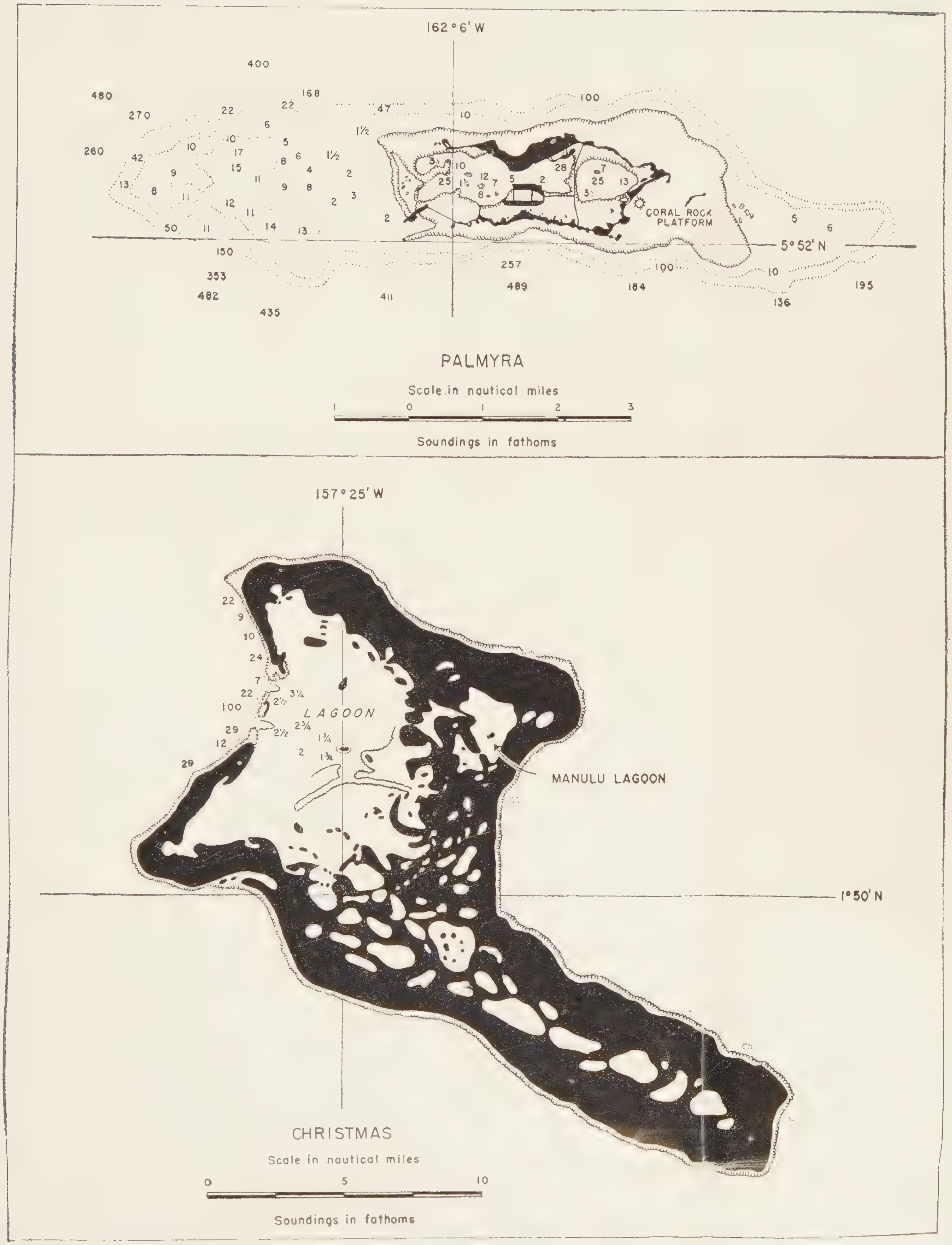

162°6' W
5°52' N
CORAL ROCK PLATFORM
PALMYRA
Scale in nautical miles
1 0 1 2 3
Soundings in fathoms
157°25' W
1°50' N
LAGOON
MANULU LAGOON
CHRISTMAS
Scale in nautical miles
0 5 10
Soundings in fathoms

FIGURE 4 - CHRISTMAS AND PALMYRA ATOLLS (from U.S.H.O. Chart No. 1839)

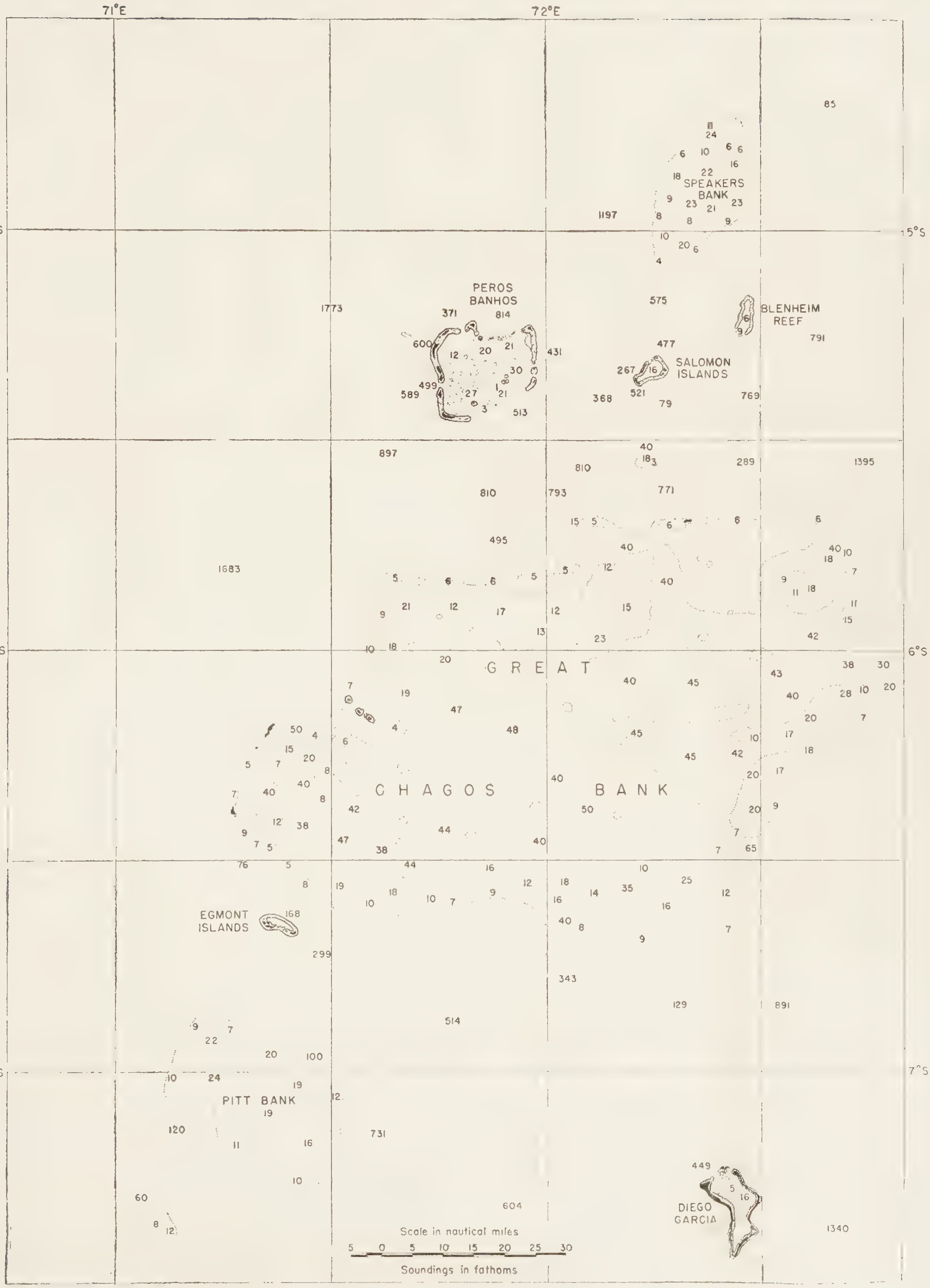

71°E
72°E
5°S
6°S
7°S
SPEAKERS BANK
PEROS BANHOS
BLENHEIM REEF
SALOMON ISLANDS
GREAT CHAGOS BANK
EGMONT ISLANDS
PITT BANK
DIEGO GARCIA
Scale in nautical miles
5 0 5 10 15 20 25 30
Soundings in fathoms

Figure 5. CHAGOS ARCHIPELAGO
SHOWING ATOLLS AND SUBMERGED
RIMMED BANKS
(from U.S.H.O. Chart No. 3869)

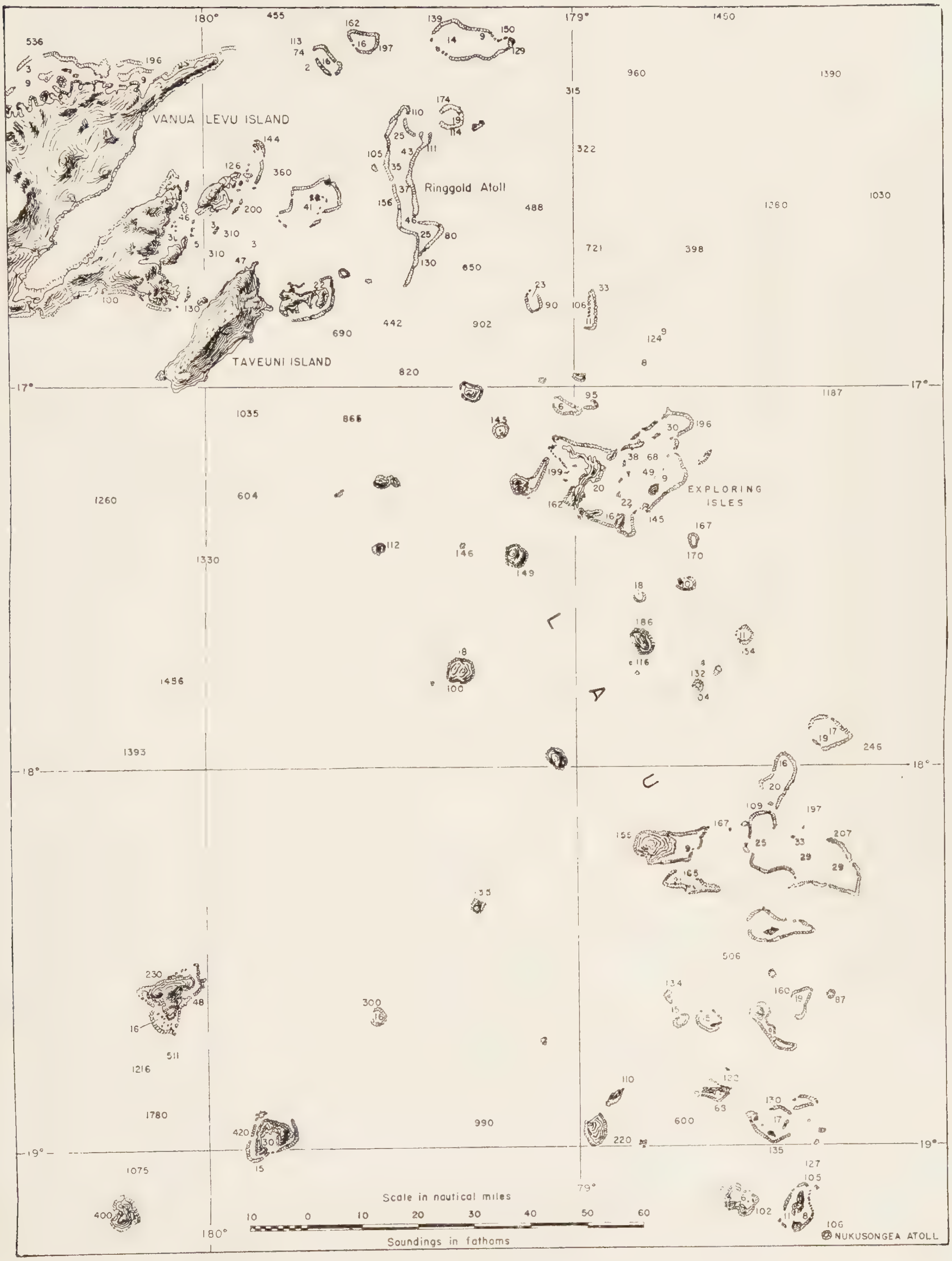

180°
179°
17°
18°
19°
VANUA LEVU ISLAND
TAVEUNI ISLAND
Ringgold Atoll
EXPLORING ISLES
L
A
U
NUKUSONGEA ATOLL
Scale in nautical miles
10 0 10 20 30 40 50 60
Soundings in fathoms

FIGURE 6.- PORTION OF EASTERN FIJI REEF-TRACT, SHOWING APPARENT INTERGRADATION OF REEF TYPES (from U.S.H.O. Chart No. 2850)

SOILS, VEGETATION AND AGRICULTURE ON CORAL ATOLLS *

By F. R. Fosberg
Pacific Vegetation Project, National Research Council
Washington 25, D.C., U.S.A.

If current theories of a post-glacial xerothermic period and consequent world-wide sea level approximately 2 meters above the present one are sound, at least the greater part of the land on coral atolls is of very recent origin. Most estimates of the time since sea level started to fall allow only a very few thousand years since the maximum level. The most recent age determination is about 3500 years or less based by Heusser on carbon 14 tests (*Ecol.* 34: 637–640, 1953). If we can assume that all present land less than 2 meters above sea level was at that time submerged or awash, little dry land could have existed on the atolls then. Most atoll features more than 2 meters above sea level seem to be of very recent storm-deposited or wind-blown loose sediments.

Granting these assumptions we may visualize soil-forming processes on atolls to have become operative only within the last few thousand years. These processes have worked, during this time, principally on a series of small, practically flat surfaces of loose and shifting, or more rarely, consolidated "coral" sand and gravel. This was composed largely of skeletons or fragments of skeletons of marine animals and plants, with, perhaps, some silt of precipitated calcareous material and a tiny increment of drifted pumice. Except for the pumice, the material was almost entirely calcium carbonate and magnesium carbonate, with the proportion of the latter variable but small.

Weathering of such material consists principally of its solution by rainwater. Because the material of an atoll islet is extremely porous and because the ground water body is affected by the tides, which increase circulation and flush away the dissolved material, such weathering and leaching does not in itself contribute much to the formation of a soil. It is ordinarily only with the help of plants and land animals that a differentiated soil may form on an atoll. In most atoll soils the only visible change from the parent calcareous sand and gravel is a darkening of the top layers by addition of humus.

---

* Approved for publication by the Director, U.S. Geological Survey.

Colonization by a dozen or so common widespread species of strand plants often takes place very rapidly on newly exposed coral sand or gravel just above high tide level. These plants are evidently not much inconvenienced by having their roots bathed occasionally by salt water. They are usually accompanied by a layer or crust of microscopic blue-green algae. Together these add humus to the calcareous material. At the same time, sea birds are very likely to rest on these land surfaces often in large numbers, adding nitrogen and phosphorus to the calcareous material and humus. Thus the principal ingredients of a soil are brought together, and conditions become more favorable for further colonization by other plants and land animals.

In this way, it can be imagined, the raw calcareous sediments recently emerged from the sea gradually assume the character of very young soils with weakly expressed morphology. The above processes continue, becoming slightly more complicated with the addition of more plant colonists and various soil dwelling animals. The soil biota of atolls is not at all well known, but doubtless plays much the same important part in soil genesis and soil maintenance that those of other soils do. It differs, though, in one important respect from biotas of most well-known soils. Land crabs and hermit crabs are among its most obvious and active members. Their effect in converting organic remains into simpler compounds and in mixing the components of the soil can hardly be overestimated.

Investigation of atoll soils reveals that, like many soils, they are made up of layers of material of different colors and textures. However, these only in small part correspond to the soil horizons used in describing ordinary soil profiles. With the exception of a darkened layer, or A_1 horizon at the surface, and several others found only occasionally, the layers are merely depositional beds or strata. The ordinary exceptions are A_{00} and A_0 horizons of organic material on the surfaces of soils of small extent in marshes, taro pits and the A_{00} and A_0 horizon of the *Jemo* soil series. In the *Jemo* series also, is an indurated B horizon. Normally, all of the other beds beneath the A_1 horizon make up the C horizon of hardly altered parent material. Darkened layers occasionally occur in the C horizon that are interpreted as buried A horizons, old surface layers covered by storm-cast calcareous debris—sand, gravel, or rubble. Most atoll soil profiles are thus simple A-C profiles. The principal exceptions are those of the phosphatic soils of the *Jemo* series, which may be described as A_0-B-C profiles.

Three principal soil series are represented on the atolls so far studied, the *Shioya,*[1] *Arno Atoll,* and *Jemo* series. Besides these there are large areas of "stony and very stony complex," of exposed indurated reef and beach limestone, and of completely unaltered calcareous sands and gravels; there are marshes and muck-bottomed taro pits, also mangrove swamps and depressions with fresh- or salt-water peats in small areas but of wide occurrence on these islands. There are, further, several minor soils described from Arno Atoll, Marshall Islands, but not yet found elsewhere.

---

[1] Shioya is a series correlated by the U.S. Department of Agriculture.

The *Shioya* series, first described from Okinawa, is found on many coral atolls and is by far the most general and widespread series of soils on these islands. Its members may be described as slightly altered lime sands or gravels, rarely loams or silts. The upper layers are gray brown or brownish gray, with values of over 4 in the Munsell soil color scheme. The organic matter content is generally quite low, except where the soils may be filled with roots. Being generally very porous, these soils have excellent or excessive drainage. The slightly colored A_1 horizon varies greatly in thickness and often changes gradually, sometimes abruptly, to unaltered sediments. This series is clearly the first step in the formation of most other atoll soils.

The *Arno Atoll*[2] series first described from Arno Atoll, southern Marshalls, includes well drained, calcareous, coarse-textured black or very dark soils with a high organic matter content. They are known from various atolls in the Marshall group, and doubtless will be found to occur in other regions.

The profile consists of a layer variable in thickness up to 50 cm. or more of altered material of a dark color, with values of less than 4 in the Munsell system, lying on unaltered or little altered lime sediments of indefinite thickness. The transition may be abrupt or gradual.

These soils, as observed in the Marshalls, are usually associated with rather intensive or long continued human activity. It is possible that their origin may be related to this activity or that more than one origin may be involved. The existence of such a soil on uninhabited Jemo Island gives weight to the speculation that cultivation of soils of the *Jemo* series may give rise to some *Arno* soils.

Most known *Arno* soils are planted to coconut groves. In several localities these groves are in very poor condition and most of the trees are dead or dying. In at least one place this condition is associated with a phosphate deficiency in the soil (Stone, *Atoll Res. Bull.* 5: 43, 1951).

The *Jemo* series, described by Fosberg (Soil Science 1954, in press) from the northern Marshall Islands, includes phosphatic soils, usually with an indurated B horizon and an A_0 horizon of raw humus. Soils of this nature are known from various islands in the Marshall group and from scattered localities in other groups of coral atolls throughout the Pacific and may occur on islands in the Indian Ocean. These soils are always found in areas occupied or recently occupied by *Pisonia grandis* forests.

---

[2] First described as the *Arno* series by Stone (*Atoll Res. Bull.* 5: 22-25, 1951), but because of the existence of an earlier *Arno* series in Texas, renamed at Stone's suggestion the *Arno Atoll* series (Fosberg, Soils of the northern Marshall Atolls, Soil Science 1954, in press).

The typical profile consists of an A_0 horizon of raw humus, acid in reaction, as much as 15 (or even 30) cm. thick, and usually underlain by an indurated layer or hardpan of phosphatic material, the B horizon, usually 5 to 20 cm. but in extreme cases to 60 cm. thick, which lies on essentially unaltered sands and gravels of indefinite thickness.

The phosphatic nature of this soil unquestionably results from the addition of excrement of sea birds that roost and nest in the *Pisonia* trees. The phosphates from the excrement, when acidified by the humus, dissolve in rain water, precipitating out when washed down into the calcareous sand, cementing the sand grains together.

The *Jemo* series seems to be the only recorded instance of the accumulation of a "raw humus" layer on a well-drained lowland tropical soil. Peats are known from waterlogged soils, but the *Jemo* series is always on loose sands and gravels. Places are known, however, where the hardpan layer may cause a temporarily perched water table. This is not a common occurrence, however. The reasons for the accumulation of humus are not clear, though the high acidity would certainly inhibit the growth of many organisms that cause decomposition. Humus from trees other than *Pisonia,* though deposited under seemingly identical condition, does not accumulate. And the humus layer disappears in a short time after *Pisonia* forest is cleared. Apparently a rather delicate equilibrium exists here between accumulation and decomposition.

The deposits of the *Jemo* series are the sources of the commercial phosphate or "guano" mined in at least the wooded atolls during the past century. Mining was still being done by the Japanese on Ebon Atoll, southern Marshalls, up to the beginning of World War II. It is not felt, however, that phosphate mining should be continued on an export basis, since phosphate deficiencies are beginning to manifest themselves locally in the Marshalls and the material might be of extreme usefulness there in the relatively near future.

The vegetation of coral atolls does not seem especially well correlated with soil types, except for the correspondence of the *Jemo* series with *Pisonia* forest, of muck with taro patches, and of peat with mangroves. More correlated might, of course, be evident, if the original vegetation were better known. Most of this has been replaced by coconut plantations, which are established indiscriminately in most situations which are not too dry, exposed, or saline.

At the present time coconut plantations might well be regarded as the characteristic vegetation of atolls. Although coconut trees are not considered to have been a part of the original vegetative cover of atolls, at least in the Pacific, there are, today, few atolls except the driest ones, that are not largely dominated by these planted palm forests. The trees may be spaced irregularly, by sporadic native planting or by germination of fallen nuts, or they may be in a regular geometrical pattern or in lines extending from lagoon to sea. The plantations may be crowded or widely spaced, and may vary from luxuriant, in the wet atolls, to spare and open in the drier areas. In luxuriant groves the canopy formed by the crowns of the trees is complete, but under less favorable conditions much sunlight may reach the ground. In well-tended plantations the undergrowth is restricted to a ground cover of grasses, *Fimbristylis, Euphorbia,* and other herbs, especially various introduced weeds. More commonly there is a thick tangled underbrush of *Wedelia, Clerodendrum, Ipomoea,* and various shrubs and saplings of trees. The underbrush, if further neglected, grows up to a tangled second story of small trees, often choked with coconut seedlings.

On wetter atolls, especially in the Caroline Archipelago, the coconut plantations may be mixed with great breadfruit trees, or may give way entirely, in places, to solid dense-canopied breadfruit groves. These usually form such a heavy shade that few plants can grow beneath them. In at least one such grove, on Nomwin Island, the ground is covered by a vinelike species of *Piper* and ferns.

Several types of native forest and scrub are known from atolls. The most widespread is a variable mixture of about a dozen kinds of trees, including *Guettarda speciosa, Pandanus tectorius, Messerschmidia argentea, Pisonia grandis, Ochrosia oppositifolia, Intsia bijuga, Pipturus argenteus, Soulamea amara, Terminalia samoensis, Allophylus timorensis, Cordia subcordata,* and *Barringtonia asiatica.* This forest may be sparse to extremely dense, low and tangled to tall and open beneath. The species may be gregarious or completely mixed. The forests may vary locally to mixtures of only a few of these species, and, frequently, to pure stands of almost any one of them. Pure stands of *Pisonia* are a conspicuous feature of atolls in many parts of the Pacific, and are associated, as noted above, with the accumulation of raw humus and the formation of *Jemo* soils. This *Pisonia* forest seems to be a relatively stable and permanent type of forest, which would perhaps be called a "climax." It reproduces itself mainly by root sprouts. However, at least in certain situations of medium rainfall, this type may be successfully invaded and eventually eliminated by *Ochrosia oppositifolia,* the necessary condition being the accidental carriage of a fruit of this species into the forest, perhaps by storm waves.

Pure forests of *Ochrosia* are found, at least, in the Marshall Islands, and form what appears to be an extremely stable, self-reproducing type, with a dense layer of seedings ready to replace fallen trees. However, one feature noted in a number of places that may belie this stability is the existence of small areas where the *Ochrosia* trees are persistently chlorotic, for at least some years, and even tend to die out and be replaced by other species. The cause of this is not at all understood.

On platforms of reef-rock and ridges of beach-rock, even where covered by extremely high tides, pure stands of *Pemphis acidula* are commonly found. These stands grow up, even in a very few years, to dense thickets 4 to 6 m. tall, penetrated with difficulty because of the stiff hard wood of even small dead branches. The small leaves and dense branching habit of *Pemphis* have occasionally given rise to reports of coniferous woods on certain atolls.

Around the windward sides of atoll islets in the trade-wind belts a band of dense scrubby mixed forest, often very largely *Messerschmidia* and *Guettarda,* usually crescentlike in outline, is commonly left by the natives as a windbreak to protect their coconut plantations from wind and salt spray. This forest slopes evenly down toward the windward, changing to low scrub, with ordinarily a fringe of bushy *Scaevola* around the edge. The leeward sides of atolls usually also support a narrow belt of *Scaevola* and occasionally other shrubs, but in profile this belt ends abruptly, with the edge either rounded or perpendicular, rather than sloping to the top of the beach.

Mangroves may occur on atolls either in shallow water or lagoon shores or in internal depressions. The depressions may be connected with the lagoon, in which case the trees may be *Rhizophora,* or have no outlet, when the trees are more usually *Bruguiera* and *Lumnitzere,* sometimes *Intsia* and *Pemphis.* At least in the Marshall Islands depressions with *Bruguiera* may have had their origin in plantings made in abandoned taro pits by the Marshallese who utilize the tree for dye-making.

On the drier atolls such as those in the belt of equatorial calms and those in the extreme northern Marshalls, forest vegetation is less well developed or absent. *Pisonia* forests may be found, but more commonly the woody vegetation is a low open scrub or scrubby forest of *Messerschmidia.* This is common on Wake Island, on Pokak Atoll, and in some parts of Christmas Island. On Pokak and Christmas Islands there is scrub of *Scaevola,* or of *Sida fallax,* the *Sida* in places forming a dwarf scrub with *Heliotropium anomalum.* Open sandy areas may have bunch-grass vegetation of *Lepturus*, whereas rocky places may have *Boerhavia* and *Portulaca lutea*. Often there are mixtures of these latter three with several other herbaceous species, or elsewhere with *Heliotropium* and *Sida*.

In general, the natural vegetation of coral atolls is of a strand character, very poor in species, especially so where the climate is dry or where the islands are very remote from other land. A rough concentric arrangement may often be observed, with more mesophytic types toward the centers of larger islets. This arrangement seems to be correlated, at least to some extent, with salinity, either of ground water or from ocean spray. The vegetation in the more protected or more central locations, and on the wetter atolls tends to approach a mesophytic forest, and on the outer parts, narrow islets, and on the drier atolls is more extremely halophytic. There seems no doubt that even on the wetter atolls the plants must be to some extent salt-tolerant, as during storms and typhoons even the most protected places may be drenched with spray or waves from the sea. The elimination of the salt-susceptible species may well be partly responsible for the extraordinarily small floras of low coral islands, but the extreme youth of the land surfaces may be an equally important factor, since chance colonization by seeds carried across large expanse of ocean must be a very slow process.

Agriculture on atolls is extremely limited, compared with that on high islands. A very few salt-tolerant economic plants are commonly grown, and it is significant that the advent of Europeans has resulted in very little change or diversification of the aboriginal forms of agriculture. A few plants, such as the papaya and squash, were added to the list of common food plants, and a number of new ornamentals became widespread. Weeds became abundant. But no new cultures were introduced. On the contrary, on many atolls the effect has been to cause the disappearance of most of the older crops and to expand the coconut culture into almost a monoculture.

There are two basic forms of agriculture, or more properly, horticulture, on atolls—dryland culture and marsh or pit culture. Both are found almost throughout the important coral island areas.

The four principal dryland food plants on these islands, are the coconut, breadfruit, pandanus, and island arrowroot or *Tacca*. Coconuts are found throughout the atoll areas that are considered habitable by the native peoples. The greater part of the land surface is covered by coconut plantations. The nuts are the basic food of practically all atoll peoples, and copra, the dried meat of the nuts, is the only export crop. The water from green nuts is generally used in place of drinking water, and the fermented sap from the cut inflorescence is the local alcoholic beverage. The trunks, leaves, and fiber from the husks are principal building and cordage materials, and husks are the principal fuel.

As practiced, coconut culture on atolls consists of planting nuts by placing them on the ground, of keeping the weeds more or less under control, and of harvesting the nuts. In a few places coconut husks and, more rarely, drift pumice are piled around the bases of the trees for fertilizer. Apparently some selection of nuts for planting has been occasionally practiced, but to no great extent. Several pests, especially insects and rats, cause some damage, and at least two kinds of trouble, possibly diseases, possibly deficiencies, weaken or kill trees. As yet little is known about these. Essentially commercial copra culture is still in the stage of an exploitation agriculture whose consequences are not yet beginning to be strongly felt. There are a few signs, though, that this will not be so forever.

Agriculture other than copra culture is carried on for subsistence only. Breadfruit culture is practiced in most islands where there is moderate or heavy rainfall. It is important in the southern Marshalls, and especially in the Caroline atolls. The breadfruit trees are planted among the coconut trees or in pure stands and eventually tower above the average coconut trees. They reach enormous sizes and produce by far the largest timber found on atolls. Their trunks are used occasionally for canoes, but generally the trees are not cut, because they are so important as a source of food.

Planting is usually by transplanting of root sprouts, at least for the seedless varieties. Those with seeds produce abundant seedlings. Both types are widely grown and used, but the seedless variety is more common. Different varieties have different fruiting seasons, which overlap and, together extend through the wetter parts of the year, at least in the Marshall Islands. In most islands, especially the Carolines, fermentation methods are used for preserving breadfruit for use during the nonbearing season.

Pandanus tectorius is one of the most widespread of atoll plants and exists in a multitude of varieties, many of which have been described as species. There are large wild populations of *Pandanus*, which reproduce by seed. Most of these are small fruited and with pulp so acrid as to be very unpleasant to eat but which may be eaten in time of famine. Their leaves are used for thatch and occasionally for plaiting. Throughout the Pacific atoll region special varieties of *Pandanus*, mostly apparently sterile, are planted for their leaves, which are especially suitable for plaiting of mats, hats, and other articles. In the Caroline, Gilbert, and Marshall Islands a considerable number of varieties with large fruits are planted for their edible pulp. These are distinguishable by the shape of the segments of the fruits and by the sweetness and flavor of the pulp. They are propagated vegetatively by breaking off small branches and sticking them in the ground. The Marshall Islanders say that if seeds of these are planted the trees thus produced are of the small-fruited wild types, called by them "erwan." Although *Pandanus* fruits are generally eaten fresh, confections and cakes are also made from them, especially in the Gilbert Islands. So dependent on *Pandanus* were the aboriginal Gilbert Islanders that they were called, by Sir Arthur Grimble, "a pandanus people."

The only other dryland food plant of much original importance was *Tacca leontopetaloides,* the Polynesian or island arrowroot. This is found throughout the atoll region, growing wild, usually in the coconut groves, and is harvested by the people. Whether the island arrowroot is ever deliberately planted is not known, but it seems to require no care at all. The tubers closely resemble potatoes in appearance, and from them is made a starch that is used in cakes, puddings, and confections. The tubers are bitter and the starch must be washed carefully. The use of *Tacca* was apparently more important in drier atolls, where taro culture was more difficult. It has now become much less common, as other starches are available.

Since the Europeans came, papayas, limes, squash, and a few other dryland plants have been introduced. Bananas, known before in some atolls, have become more widespread. They are rather sensitive to salt, however, and do not do especially well except in the interior of wet islets. They are also sometimes planted in pits.

Taro pits are a widespread feature of atolls, except in the driest areas. They are dug in various forms, from small circular or oblong depressions to great fieldlike areas and long winding ditches. Essentially, however, all are alike in being excavated below the water table and filled with organic matter which decomposes into a soft fertile muck continually wet with ground water that rises and falls with the tides. The muck, in most places, is constantly replenished by adding vegetable matter of all sorts. In the Gilbert Islands weeds and leaves are carefully saved and dried for this purpose. Pumice is also added to the muck in some atolls. The principal plants raised in these pits are two aroids that are cultivated for their starchy corms, the giant taro *Cyrtosperma chamissonis,* and the taro *Colocasia esculenta.* Both are very important food plants capable of supporting many people on very small acreages. Planting materials used are the upper parts of the corms or small branches and tubers produced on their sides. *Cyrtosperma* apparently does not require much replanting and can crowd out the *Colo-*

casia unless carefully controlled. *Colocasia* is generally replanted when harvested. Many varieties of each of these plants exist, but their taxonomy has never been adequately studied.

Other plants, especially sugar cane and occasionally bananas, as well as even ornamentals such as hibiscus, are planted occasionally in these pits, but these are minor crops.

In the northern Marshalls, and even to some extent in the southern Marshalls, this type of agriculture has disappeared, probably because it has been easier to make copra and sell it and buy rice and flour for starch requirements. In such atolls as Ailuk, Likiep, Lae, and others, there are extensive long-abandoned pits, now mostly dry and partly filled, with full-grown coconut and breadfruit trees growing in their bottoms. The large pits and the trees give an idea of the former extent of this culture and the length of time it has been abandoned. In 1946 an attempt was made to revive taro culture in the northern Marshalls, especially on Likiep, Ailuk, and Lae. Planting material was secured from the southern Marshalls and much interest was displayed in the project. By 1951, however, it had been almost completely abandoned. The complaint was made that it was too much work to keep the pits free from weeds. It was observed that the principal weed in most of the abandoned pits was *Paspalum vaginatum*, a very vigorous sod-forming, recently introduced grass, which favors brackish places. Doubtlessly the aggressive nature and persistent habit of this plant are largely responsible for the failure of this experiment. It is hoped that *Paspalum vaginatum* will not become more widely introduced into the atolls that depend on taro for an important part of their food supply. Another giant aroid, *Alocasia*, used only as a famine food, is also found as a troublesome weed in taro pits, and will, if left alone, crowd out the useful taros.

Little has been said about the reasons for the restricted number of agricultural plants found in atolls, because little is actually known about the subject. Salinity is suspected as one reason for failure of most garden plants to grow, but the problem is not as simple as this. So little is known about the fertility of the soils of atolls that any discussion of the subject would be mere guessing. It is a fact, however, that most ordinary garden plants have been tried and few of them have grown at all. Stone (1951) found deficiencies of several essential elements. High salinity, high calcium carbonate content, and various deficiencies might be sufficient reason for poor results in gardening.

Increasing populations on many atolls are surely going to strain the food production capacity of these islands before very long. The problem will not be solved by utilizing new land, as there is not much unoccupied land to be had, and what there is mostly on dry atolls or on tiny, very saline islets on other atolls. Therefore, development of a more productive agriculture would seem to be the only hope of maintaining self-sufficiency in these microcosms. Beyond a slight attempt at selection of coconuts for planting, no beginning has as yet been made toward agricultural improvement. In aboriginal times, obviously, there was selection in most of the economic plants, as many varieties with different horticultural characteristics exist in the different atolls. But the resources of modern plant-breeding have never been brought to bear on any of the problems in these islands. Though in most atoll groups, except the Gilberts, there is not yet serious overcrowding, it might be well to think about these matters before the emergency arises. Any plant-breeding or crop-improvement program is a longterm undertaking and should be started well before results are needed. As a general guiding principle it might be suggested that it would be best to devote such work to the improvement of the food plants now used in the atolls. These plants, at least, are adapted to a saline environment and will definitely grow there. Also, the people are already accustomed to using them.

RELATION OF HUMANS TO THE ATOLL ENVIRONMENT

By Alexander Spoehr
Bernice P. Bishop Museum
Honolulu 17, Hawaii

The present paper is in no sense a definitive report on the results of the work of the Coral Atoll Program in the field of human ecology. Most of the data obtained are still in process of preparation for publication, and until the reports of the various atoll teams are in fact published, no final conclusions can be drawn regarding the work accomplished in the human ecology of coral atolls. The following remarks represent my personal views regarding the progress that has been made under the Pacific Science Board's Coral Atoll Program.

The Atoll Program has been conceived as the ecological study of a total environment, within which man has been regarded as merely one of a complex of related elements. Although it is merely a personal article of faith, I am in complete agreement with Marston Bates' stand that ecology is essentially a point of view—a point of view that stresses the relationships among the elements or terms of a system. Unfortunately, when one examines the relationship between a human population and its natural environment, as expressed on a coral atoll, certain characteristics of *homo sapiens* introduce factors that are very difficult to cope with in setting up problems for investigation in the field. The most important of these factors is that man is not only a social animal, in the sense that many vertebrates are social, but is also characterized by that entity called culture—the body of techniques, beliefs, and particular social patterns that are transmitted through tradition and which are constantly changing their configuration, both in time and space. The human population of a coral atoll adapts itself to the atoll environment through the medium of its culture. Field work in human ecology cannot ignore this fact and must develop its methodology accordingly.

From the viewpoint of human ecology, a matter of first importance is that the Atoll Program has resulted in a much fuller and more detailed understanding of the coral atoll as an environment for human occupance. It is obviously impossible to examine the relationship of any human population to its environment without a knowledge of the principal characteristics of that environment and of their inter-relationships. The individual studies that have been centered on the physical and biological characteristics of atolls provide the necessary foundation for fruitful work in human ecology, even if the pursuit of the latter has, in the Coral Atoll Program, raised more problems than it has solved.

It must also be remembered that man came to the atolls of the Pacific as a migrant, bringing with him a distinctive biotic assemblage of cultivated plants and domestic animals, as well as hangers-on in the form of plant weeds, the rat, and human parasites. This biotic assemblage has itself become part of the total environment of the atoll-dweller, and has, of course, been augmented in historic times with new introductions of plants and animals. An achievement of the Atoll Program is a fuller understanding of the manner in which this distinctive biotic assemblage has become incorporated into the atoll environment, and of the physical factors, such as soils and ground water, that make possible the continued existence of major elements of this biotic assemblage, which in turn are essential for human survival. Those coral atolls inhabited by man have for untold centuries presented what Marston Bates has called a "managed landscape," in that numerous important plants contributing to this landscape are controlled by man. How this "managed landscape" first took form and came into being can only be inferred, but we at least are in the position of understanding the significance of the human factor in affecting the changes that have taken place.

An important aspect of ecological study is the determination of external factors that control the survival and size of populations. The coral atoll imposes certain conditions that must be met by the atoll dweller. The most important of these is that, given the technology obtaining prior to the extension of modern commercial economy to the Pacific Islands, atoll populations had to make a successful adaptation to both land and sea. For this reason, figures on population size and density for coral atolls mean little unless it is realized that the adaptation of atoll peoples in the past was, and often still is, based on a joint dependence on both land and sea resources. As a result of the Atoll Program, we are now in a much better position to assess the extent and nature of these resources for human use. The atoll environment is certainly not as forbidding as it has sometimes been made out to be. On none of the four atolls studied has there been a complete utilization of all potential food resources, nor on any atoll does the food quest consume all men's time and energy. Nevertheless, the pressure of population on land resources can be clearly seen in a few atolls, such as Mokil in the Carolines.

I cannot help but feel that there is a further concomitant of the atoll dweller's joint adaptation to land and sea. It is no accident, I believe, that atoll peoples were known throughout the Pacific islands for their skill as canoe-builders, seamen and navigators. Furthermore, in contrast to high islanders, under modern conditions of acculturation, atoll dwellers have tended to retain a familiarity with the sea, even though a modern Marshallese canoe captain may use a compass, a U. S. Hydrographic Office chart and a sextant to navigate, rather than to use the empirical lore of his ancestors. The atoll environment has been conducive to stimulating and preserving adaptation to the sea.

That the characteristics of the atoll environment are reflected in other aspects of atoll culture remains to be demonstrated. The technology, economy and features of social structure whereby resources are controlled, production and exchange organized, and subsistence patterned, are all shared by high islanders in a widespread Micronesian and Polynesian pattern. Such differences as do characterize atoll dwellers seem to be more of degree rather than of kind.

The ecological approach to the study of atoll populations pays special attention to the manner in which environmental factors shift in importance under different cultural circumstances. One of the difficulties of the study of atoll populations is the lack of time depth that we possess, with respect to the cultural changes that have taken place on atolls, in relation to environmental factors. The nature of interdependence among the variables of any system is generally most clearly evident under changing rather than under static conditions. As compensation for the lack of time depth in atoll studies, an attempt has been made under the Atoll Program to carry on field research on atolls with differing characteristics.

Four inhabited atolls have been examined under the Program: Ifaluk, Onotoa, Arno, and Raroia. Prior to western contact, the cultures of these four atoll societies had certain major features of technology, and economic and social organization, that were basically similar. With the extension of the copra economy to the Pacific islands, and under other western influences, these four atolls now exhibit differing degrees of acculturation. Of the four atolls studied, Ifaluk has been least affected, Raroia probably most affected, with Onotoa and Arno in between.

With the development of the copra economy, the more affected atoll dwellers have tended to import foods such as rice and tinned fish, to neglect their former food resources, and even to forget a considerable part of the technology once used to exploit these resources. This specialization in the production of copra has in turn resulted in a greater vulnerability of the more acculturated atoll populations to environmental disturbance. Although no one would wish to deny atoll dwellers certain of the benefits of contact with contemporary civilization, from the viewpoint of the human ecologist the more acculturated atoll societies exist, by virture of their specialization, in a more vulnerable and precarious relationship with their environments than do their less acculturated cousins.

Cultures, no matter how isolated their human carriers, never remain static and unchanging. The processes of acculturation, whose effects are exhibited in differing degrees on the four atolls examined, will continue. Nevertheless, all these atolls do impose on their inhabitants environmental limitations that cannot be transcended by future culture change. The inter-action between these limitations and such culture change as is now in process forms an important problem for future examination.

Apart from such contributions to knowledge as may result from the Atoll Program, it has also been an important adventure in team research. The extent to which the contributions of the individual investigators can be welded into integrated wholes that do in fact advance knowledge of the ecology of atolls, must await publication of the final results of the field work. Experience during the program has indicated that in the functioning of the research team, the anthropologist, who was most immediately concerned with human ecology, was most valuable in a supporting role, whereby he maintained effective liaison with the local community for the benefit of the team as a whole. On the other hand, anthropological field work is by its nature extremely time-consuming, particularly where the accumulation of quantitative data is involved. Under these conditions it seems likely that the contributions of the non-anthropologists may well be more significant than those of the anthropologists. It can, however, be anticipated that the Coral Atoll Program, at the very least, will provide a sharper sense of the kinds of problems that can be fruitfully investigated in the field of human ecology as a whole, and a more realistic appraisal of appropriate methods to be used—of both of which the study of human ecology is sorely in need.

CRUSTACES DECAPODES PAGURIDAE D'OCEANIE FRANCAISE

Par JACQUES FOREST

RÉSUMÉ

La collection de Paguridae récoltée en 1952 par M. G. Ranson dans la zone intercotidale des îles de Tahiti, d'Hikuéru et de Takumé, comprend plusieurs milliers de spécimens appartenant aux espèces suivantes: *Clibanarius corallinus* H. Milne-Edw., *C. humilis* Dana, *C. striolatus* Dana, *Calcinus elegans* H. Milne-Edw., *C. gaimardii* H. Milne-Edw., *C. herbstii* de Man, *C. latens* Randall, *C. seurati* Forest, *Pagurus deformis* H. Milne-Edw., *P. gemmatus* H. Milne-Edw., *P. megistos* Herbst, *P. sanguinolentus* Quoy et Gaimard, *P. scutellatus* H. Milne-Edw., *Aniculus aniculus* Fabr., *Coenobita hilgendorfi* Terao, *C. perlatus* H. Milne-Edw., C. *rugosus* H. Milne-Edw., *Birgus latro* L. A cette liste s'ajoutent *Clibanarius ransoni* sp., nov., *Eupagurus anceps* sp. nov., *Catapaguroides? trichophthalmus* sp. nov., et *Clibanarius zebra* var. *rhabdodactylus* var. nov.

Les coquilles avaient été déterminées par M. Ranson: il semble que les pagures recherchent avant tout des coquilles à leur taille, mais certaines espèces s'accommodent mieux que d'autres de coquilles à ouverture étroite (*Conus* par exemple) et subissent souvent, à la suite d'un séjour prolongé dans ce genre d'habitation, un aplatissement dorsoventral parfois très accentué.

L'examen de plusieurs types conservés au Muséum de Paris a permis d' établir plusieurs synonymies (en particulier: *Pagurus euopsis* Dana = *P. sanguinolentus* Quoy et Gaimard, *P. fabimanus* Dana = *P. scutellatus* H. Milne-Edw.).

Parmi les espèces nouvelles décrites, *Eupagurus anceps* sp. nov., espèce de très petite taille, présente un important dimorphisme sexuel: la pince droite est beaucoup plus grosse et de forme différente chez le mâle. *Catapaguroides? tricophthalmus*, représenté par un seul spécimen mâle mutilé, a une position générique qui ne sera précisée que lorsque la femelle aura été découverte.

Les Pagurides étudiés ici ont été recueillis de mai à octobre 1952 par Monsieur G. Ranson du Muséum National d'Histoire Naturelle au cours d'une mission à travers les Establissements Francais d'Océanie. Tous, à une exception près, proviennent de Tahiti ou de deux îlots de l'Archipel des Tuamotu: Hikuéru et Takumé. Ils ont été capturés sur le plateau côtier, à l'intérieur de la zône intercotidale ou à un niveau légèrement supérieur.

La collection comprend plusieurs milliers de spécimens appartenant à 22 espèces ou variétés dont quatre sont nouvelles pour la science. Le fait que sept d'entre elles soient représentées par un grand nombre d'individus—plus de deux mille pour *Clibanarius humilis Dana* et plusieurs centaines pour les autres—est particulièrement intéressant. Il faut constater une fois de plus que, chez les Pagures, certains caractères habituellement utilisés dans les diagnoses varient considérablement dans une même espèce, non seulement suivant l'âge et le sexe, mais, à taille égale, d'un spécimen à l'autre. S'il est nécessaire de tenir compte des proportions relatives des pédoncules oculaires, antennulaires et antennaires, aussi bien que du rapport des longueurs dactyle-propode des pattes ambulatoires, il faut préciser que l'on ne fournit que des moyennes, valables pour des individus adultes. Par contre, l'importance des marques colorées comme caractères spécifiques apparaît de plus en plus: il ne s'agit pas de la coloration elle-même qui varie parfois considérablement suivant le mode de fixation et, en général, devient moins intense après un séjour plus ou moins long dans l'alcool, mais de la disposition des bandes et taches sur la carapace et les appendices céphaliques et thoraciques.

Les coquilles avaient été déterminées par M. Ranson, et il était ainsi possible de se rendre compte si certaines espèces de Pagurides marquaient une préférence pour certaines coquilles. Le tableau qui figure à la fin de la présente communication a été établi pour les sept espèces les mieux représentées; il montre que l'habitation est choisie avant tout, en raison de ses dimensions; si l'on prend par exemple deux Pagurides fort éloignés, un Cenobite, *Coenobita perlatus* H. Milne-Edwards, et un Pagure, *Clibanarius corallinus* H. Milne-Edwards, on constate que, dans vingt-deux cas, on les trouve dans des coquilles de la même espèce. Les Pagures de grande taille, *Pagurus* et *Aniculus*, qui ne figurent pas dans le tableau, car ils ne sont représentés que par quelques individus, sont presque toujours dans des *Turbo*, seuls logements disponibles en rapport avec leurs dimensions. De même les minuscules *Eupagurus anceps* se sont installés dans les petits Cerithes et dans les *Planaxis lineolatus* Gould dont la taille leur convenait. Dans certaines coquilles particulièrement abondantes sur le plateau côtier, vivent indifféremment l'une ou l'autre des sept espèces de Pagures ou de Cénobites retenues. C'est le cas de *Cantharus undosus* (L.) et de *Strombus floridus* Lmk. La forme de la coquille joue aussi un rôle, les petits *Conus* et les *Cypraea,* dont l'ouverture est fort étroite sont en général dédaignés, et il arrive souvent que l'on en brise un grand nombre sans en trouver une seule d'occupée soit par le Gastéropode, soit par un Pagure. Cependant, une petite espèce, *Calcinus latens* Randall semble s'accommoder particulièrement bien de ce genre de coquille, et, en particulier, des *Conus.* Une autre espèce, beaucoup plus grande celle-là, *Pagurus sanguinolentus*

Quoy et Gaimard (=*P. euopsis* Dana) vit souvent elle aussi dans des coquilles à ouverture étroite, ce qui entraîne un aplatissement dorso-ventral extrême de certains adultes. Les modifications morphologiques, conséquences de cet aplatissement, sont telles que les individus qui les avaient subies ont été considérés comme appartenant á une espèce distincte, *P. depressus* Heller. En fait il s'agit d'une seule et même espèce dont la plasticité est remarquable; *P. sanguinolentus* peut aussi se trouver dans des coquilles à large ouverture: sur trois spécimens récoltés par M. Ranson, l'un était dans un *Turbo,* les deux autres dans des cocquilles à ouverture étroite, *Pterocera* et *Conus.*

Les difficultés rencontrées pour déterminer certaines espèces ont fait apparaître la nécessité de les redécrire et de les comparer à d'autres formes indo-pacifiques. C'est dans le genre *Clibanarius* qu'il existe le plus de confusion, et une révision complète de ce groupe serait désirable. J'ai indiqué que le nom de *C. aequabilis* Dana devait être réservè à une espèce qui n'est connue avec certitude, pour l'instant, que des Iles du Cap Vert et de Madère; les spécimens de l'Indo-Pacifique signalés sous le nom de *C. aequabilis,* ou sous celui de *C. aequabilis* var. *merguiensis* de Man, appartiennent soit à une espèce qui doit être désignée sous le nom de *C. merguiensis* soit à une autre espèce. C'est ainsi que les *C. aequabilis* des Iles Gambier, déterminés par Nobili, sont en réalité des *C. humilis* Dana.

L'étude de certains types conservés au Muséum a montré que des espèces de la collection Ranson avaient été décrites bien avant qu'elles recoivent le nom sous lequel elles sont généralement connues. Le cas le plus remarquable est celui du *Pagurus euopsis* dont il a été question plus haut, espèce décrite par Dana en 1852 et bien souvent signalée depuis sous ce nom ou celui de *P. depressus* Heller, qui me paraît identique au *P. affinis* de H. Milne-Edwards et au *Pagurus sanguinolentus* du Voyage de l'Uranie, décrit en 1824 par Quoy et Gaimard. D'autre part je tiens le *P. fabimanus* de Dana, pour identique au *P. Scutellatus* de H. Milne-Edwards (1848).

Les formes nouvelles décrites ici sont de petites ou très petites formes. C'est au genre *Clibanarius* qu'appartiennent les deux premières, *C. ransoni* sp. nov. et *C. zebra* var. *rhabdodactylus* var. nov. qu'il sera peut-être nécessaire de séparer complétement de *C. zebra* Dana lorsqu'on disposera d'un matériel plus abondant. *Eupagurus anceps* sp. nov. espèce minuscule, présente un dimorphisme sexuel important dans le chélipède droit. *Catapaguroides? trichophtalmus* sp. nov. n'est malheureusement représenté que par un mâle mutilé. Il est impossible actuellement de le ranger avec certitude dans un genre *d'Eupagurinae,* et ce n'est que tout à fait provisoirement que je l'ai rattaché aux *Catapaguroides.*

Il semble que la collection de Paguridea de M. Ranson soit la plus importante qui aît jamais été rassemblée dans la région délimitée par les trois îles de Tahiti, Hikuéru et Takumé, mais il est intéressant de la comparer au matériel récolté au début du siècle à Tahiti et surtout sur les îles Gambier, relativement proches, par G. Seurat. La collection Seurat a été étudiée par Nobili (1907), elle est conservée au Muséum et j'ai revu les spécimens appartenant aux espèces présentes dans les deux collections. Nobili a signalé 21 espèces de Paguridea, qui se réduisent à 20 si on admet que *Calcinus terrae-reginae* Haswell est identique à *C. latens* Randall. 15 espèces sont communes aux deux collections; deux *Eupagurinae* décris par Nobili, *Eupagurus maorus* et *Anapagurus polynesiensis,* connus par les types seulement, un *Diogenes, D. gardineri* et deux Cénobites, *C. spinosus* H. Milne-Edwards et *C. olivieri* Owen n'ont pas été retrouvés. La liste des espèces recueillies par M. Ranson figure ci-dessous. Celles qui sont aussi présentes dans la collection Seurat sont précédées d'un astérisque, et éventuellement, suivies du nom qui leur a été attribué par Nobili quand il diffère de celui que j'emploie.

Clibanarius corallinus H. Milne-Edwards
* *C. humilis* Dana ("*C. aequabilis* Dana", Nobili)
C. ransoni sp. nov.
* *C. striolatus* Dana
* *C. zebra var. rhabdodactylus* var. nov. ("*C. zebra* Dana", Nobili)
* *Calcinus elegans* H. Milne-Edwards
C. gaimardii H. Milne-Edwards
* *C. herbstii* de Man
* *C. latens* Randall (incl. "*C. terrae-reginae* Haswell", Nobili)
C. seurati Forest
* *Pagurus deformis* H. Milne-Edwards
P. gemmatus H. Milne-Edwards
* *P. megistos* Herbst ("*P. punctulatus* Oliv.", Nobili)
* *P. sanguinolentus* Quoy et Gaimard ("*P. euopsis* Dana," Nobili)
P. scutellatus H. Milne-Edwards
* *Aniculus aniculus* Fabricius
Eupagurus anceps sp. nov.
Catapaguroides? trichophthalmus sp. nov.
* *Coenobita hilgendorfi* Terao ("*C. clypeatus* Latr.", Nobili)
* *C. perlatus* H. Milne-Edwards
* *C. rugosus* H. Milne-Edwards
* *Birgus Latro* L.

Les longueurs de carapace (L.c.) minimum et maximum ont été données pour chaque espèce. Le choix de cette dimension, mesurée du milieu du bord frontal au bord postérieur des lobes branchiaux, permet des comparaisons relativement valables entre les individus et les espèces, alors que la longueur totale qui dépend de celle d'un abdomen extensible, plus ou moins contracté et enroulé en spirale, ne présente pas une grande signification.

PAGURIDAE Dana

PAGURINAE Ortmann

Genre *Clibanarius* Dana

Clibanarius corallinus (H. Milne-Edwards 1848)

Pagurus corallinus H. Milne-Edwards, 1848 p. 63.

Clibanarius obesomanus (*? corallinus*), Dana, 1852, p. 468, pl. XXIX, fig. 8 *a-c*.

"*Clibanarius corallinus* (Edw.)", Nobili, 1907, p. 367.

Hikuéru, Tahiti et Takumé: de très nombreux individus comprenant des ♀ ovigères. L.c.: 3,5 à 25 mm.

Clibanarius humilis Dana 1851

Pagurus humilis Dana, 1851, p. 271.

Clibanarius humilis Dana, 1852, p. 469, pl. XXIXn fig. 9.

"*Clibanarius aequabilis* Dana", Nobili, 1907, p. 367.

"*Clibanarius aequabilis* var. *merguiensis* de Man", Bouvier, 1915, p. 29.

Hikuéru, Tahiti et Takumé: de nombreux individus dont beaucoup de ♀ ovigères. L.c. 2 à 11 mm.

Description.—Ecusson céphalothoracique un peu plus long que large. Rostre court, dépassant à peine l'alignement des dents latérales. Pédoncules oculaires un peu plus courts que le bord frontal et que les pédoncules antennulaires. Pédoncules antennaires atteignant ou dépassant légèrement la base des cornées. Chélipèdes dissymétrique chez les adultes: le droit plus grand et plus renflé dans la région palmaire que le gauche. Les deux appendices couverts de tubercules petits et peu sauillants dans la région palmaire, un peu plus forts et plus aigus au voisinage du bord interne et sur les doigts. Pattes ambulatoires avec le propode et le dactule, mesurés le long du bord supérieur, à peu près de même longueur. Le propode de *p* 3 gauche avec une carène bien marquée le long du bord supérieur de la face externe, et celle-ci légèrement déprimée sous la crête. Pilosité faible constituée par des poils, en général courts. Ecusson céphalothoracique blanchâtre, maculé de jaune-orange, avec en particulier une tache en arrière de chaque angle antérieur. Pédoncules oculaires jaune-orange avec un large anneau blanc sous les cornées et une grande tache blanche sur la moitié proximale. Ecailles oculaires jaune-orange. Chélipèdes orange-rougeâtre avec les tubercules bdanchâtres. Dactyle des pattes ambulatoires blanc avec les régions supérieure et inférieure légèrement teintées de jaune. Propode d'un brun violacé intense avec, sur les faces internes et externes, une bande blanche, qui prend naissance à la base de l'article et s'étend jusqu'au tiers distal au plus. Carpe brunviolacé avec une bande plus claire sur les faces latérales.

Remarques.—Par le nombre des spécimens récoltés, *Clibanarius humilis* Dana et *C. corallinus* H. Milne-Edwards, sont les espèces les mieux représentées du genre dans le matériel étudié ici. Dans la collection du Muséum, *Clibanarius humilis* ne figurait pas sous ce nom, mais sous ceux de *C. aequabilis* Dana (Spécimens des Tuamotu déterminés par Nobili) et de *C. aequabilis* var *merguiensis* de Man (Spécimens de l'Ile Maurice, déterminé par Bouvier). Ces confusions laissent supposer qu'il en existe d'autres dans la littérature, souvent impossibles à décéler, et justifie la redescription d'une espèce très largement et abondamment distribuée dans la région Indo-Pacifique. *Clibanarius humilis* possède des pédoncules oculaires dont la longueur n'excède pas la largeur du bord frontal même chez les adultes, et des chélipèdes fort peu épineux dans la région palmaire, mais les meilleurs caractères, ceux qui permettent de l'identifier immédiatement, concernent la coloration des pédoncules oculaires et des pattes ambulatoires. La face externe du propode de celles-ci présente une coloration foncée, en général brun-violacé, dans la région antérieure. Cette coloration qui offre un maximum d'intensité au bord antérieur de l'article, s'étend plus ou moins vers l'arrière, davantage près des marges mais en laissant toujours une zône beaucoup plus claire à la base.

Il n'y a pas lieu de comparer *C. humilis* avec ce que je tiens pour le véritable *C. aequabilis* de Dana qui est une espèce atlantique bien différente. Dana a décrit sous le nom de *C. aequabilis* des spécimens de Madère et des Iles du Cap Vert d'une part, de Tahiti d'autre part. Il est manifeste que le même nom couvre deux espèces distinctes. Sa description des spécimens atlantiques s'applique exactement a des *Clibanarius* récoltés à Pedro Lume, Iles du Cap Vert, (cf. Forest, Bull. Mus. Nat. Hist. Nat., 1953, *25*, n° 5). Le nom d'*aequabilis* devrait être réservé à cette espèce qui n'est connue avec certitude que des Iles du Cap Vert et de Madère. En effet, les *Clibanarius* du Cameroun identifiés à *C. aequabilis* par Aurivillius (1898), cité ultérieurement par Rathbun (1900) et Balss (1921) sont en réalité, à en juger par le dessin qu'il en donne, et comme l'a signalé Odhner (1923), des *C. senegalensis* Chevreux et Bouvier. A quoi correspond le spécimen de *C. aequabilis* de Tahiti, figuré par Dana, et dont il écrit qu'il possède des pattes bleu foncé, non rayées? Estce la forme décrite par de Man sous le nom de *C. aequabilis* var. *merguiensis?* Cela est douteux en raison de la coloration indiquée, qui ne s'applique d'ailleurs à aucum des *Clibanarius* signalés à Tahiti. Il est souhaitable que le terme d'*aequabilis* ne soit plus utilisé pour des espèces de l'Indo-Pacifique. La forme décrite avec précision par de Man ne doit pas être considérée comme une variété d'une espèce atlantique, que ce soit *C. aequabilis* ou, comme on trouve dans Melin (1939, p. 24), *C. misanthropus.* Les caractères principaux de *C. merguiensis* seront indiqués à la suite de la description d'une espèce nouvelle de Tahiti, *C. ransoni* sp. nov. On notera simplement ici que le propode des pattes ambulatoires présente chez *C. merguiensis* une coloration inverse de celle qu'on observe chez *C. humilis.* C'est la région antérieure, et non pas la région postérieure du propode qui est de teinte claire.

Clibanarius ransoni sp. nov.

Tahiti: 3 ♂ L.c. 4,5 — 5,5 — 7 mm; 1 ♀ ovigère, L.c. 4,5 mm (Syntypes) dans *Nerita plicata* L., *Strombus floridus* Lmk.

Clibanarius ransoni: Pédoncules oculaires rouge-orange avec une très large bande longitudinale d'une teinte un peu plus foncée sur la face supérieure. Les deux paires de pattes ambulatoires avec, sur la face externe, une large bande d'un blanc-bleuté nettement délimitée s'étendant de la base de l'ongle à la base du mérus.

Clibanarius merguiensis: Pédoncules oculaires rougeâtres avec une marque longitudinale blanchâtre bien délimitée, sur la face supérieure. Pattes ambulatoires rougeâtres avec, sur la face externe du dactyle, dans sa moitié proximale, une plage blanche qui s'étend plus ou moins sur le propode, parfois, pour les *p* 3, jusqu'à la base de l'article. Sur les *p* 2, cette marque blanche est limitée à la région antérieure du propode, la plus grande partie de l'article étant d'une teinte rougeâtre uniforme. Les zônes claires qui existent sur ces appendices ne se présentent pas sous la forme d'une bande continue, bien délimitée.

Clibanarius striolatus Dana 1852

Clibanarius striolatus Dana, 1852, p. 463, pl. XXIX, fig. 3 *a-c*.

"*Clibanarius striolatus* Dana", Nobili, 1907, p. 367.

Tahiti: 3 ♂, L.c. 5, 8 et 10,5 mm, dans *Cantharus undosus* L., *Strombus floridus* Lmk.

Clibanarius zebra var. *rhabdodactylus* var. nov.

"*Clibanarius zebra* Dana", Nobili, 1907, p. 367.

"*Clibanarius zebra* Dana", Buitendijk, 1937, p. 264 et 267.

Hikuéru: 3 ♂ et 9 ♀ (dont plusieurs ovigères), L.c. 2,5 à 3 mm et 1 ♂, L.c. 4,5 mm, type de la variété. Dans *Cerithium nesioticum* Pilsbry et Vanatta, *Cypraea moneta* L.

Description.—Ecusson céphalothoracique un peu plus long que large (rapport des dimensions égal à 6/7 environ). Rostre aigu, dépassant l'alignement des dents latérales. Pédoncules oculaires un peu plus longs que le bord frontal, le droit très légèrement plus court que le gauche. Pédoncules antennulaires à peu près de même longueur que les pédoncules oculaires. Pédoncules antennaires dépassant la base des cornées. Chélipèdes égaux, ou le droit légèrement plus fort que le gauche, couverts de tubercules plus saillants et plus aigus dans le voisinage du bord palmaire et sur les doigts. Pattes ambulatoires à dactyle plus court que le propode: rapport des deux articles, mesurés le long du bord supérieur, sensiblement égal à 4/5 pour les *p* 2 et la *p* 3 droite, à 6/7 pour la seconde patte gauche. Le propode de cette dernière avec une carène lisse le long du bord supérieur de sa face externe.

Des poils fins, en faisceaux, surtout sur la face supérieure des trois derniers articles des chélipèdes et sur les régions supérieures et inférieures des pattes ambulatoires.

Coloration de fond jaunâtre, avec des marques colorées rouges en général encore très vives après un long séjour dans l'alcool. Taches colorées sur l'écusson céphalothoracique disposées en quatre bandes longitudinales. Pédoncules oculaires avec une large rouge médiane sur toute la longueur de la face supérieure. Chélipèdes rouges. Pattes ambulatoires striées de rouge sur toute leur longueur: le propode avec cinq bandes régulièrement espacées dont trois sont visibles sur la face externe et qui se prolongent toutes sur le dactyle jusqu'à l'ongle.

Remarques.—Ces petits pagures sont indentiques au "*Clibanarius zebra*" récolté par Seurat à Hao (Iles Tuamotu) et déterminé par Nobili. Ils sont aussi identiques aux *Clibanarius zebra* d'Indonésie provenant de l'Expédition Snellius, dont j'ai examiné trois spécimens. Par contre ils présentent certaines différences, notamment dans la coloration, avec des spécimens récoltés à Taiohae (Iles Marquises) en 1927 par le Père Siméon Delmas, et que j'avais identifiés à l'espèce de Dana. Les deux formes sont voisines mais il est impossible de les confondre. Si je ne les ai pas rangées dans des espèces différentes, c'est que les spécimens de Taiohae sont en moyenne beaucoup plus grands que les autres et qu'il est ainsi difficile d'établir une comparaison valable entre les proportions des différentes régions du corps et des appendices. D'autre part les différences de colorations portent non pas sur une disposition différente des marques colorées mais sur l'absence de pigmentation sur certaines régions dans l'une des formes en question. Ce sont les spécimens de Taiohae, que je considère comme des *Clibanarius zebra* typiques parce qu'ils possèdent des pattes ambulatoires à dactyles non rayés, comme celui qui a été figuré par Dana (pl. XXIX, fig. 5 *d*). La forme typique diffère de la variété décrite plus haut par les pédoncules oculaires plus longs et plus grêles avec un diamètre compris plus de cinq fois dans leur longueur, par le dactyle des pattes ambulatoires plus déprimé latéralement et plus court par rapport au propode. La taille des individus provenant des Marquises, une cinquantaine environ, est comprise entre 5,5 et 11 mm (L.c.); les plus petits possèdent des pédoncules oculaires relativement courts et trapus, et des pléopodes impairs peu développés, caractères juvéniles chez les pagures. D'un autre côté, les trois spécimens d'Indonésie avaient des carapaces de 5,5 – 6 et 6,5 mm et ceux d'Hikuéru des carapaces de 2 à 4,5 mm avec, parmi les individus les plus petits, des femelles ovigères. La variété *rhabdodactylus* serait donc de taille nettement inférieure à celle du *Clibanarius zebra* typique.

Les différences de colorations sont indiquées dans le tableau ci-dessous. Nous y avons introduit une autre espèce bien proche des *C. zebra*, *C. signatus* Heller de la Mer Rouge et du nord de la Mer d'Arabie, dont les chélipèdes sont plus fortement tuberculés, mais qui porte, à peu de chose près, les mêmes bandes rouges que la variété *rhabdodactylus*.

	Clibanarius zebra typ.	*Clibanarius zebra* var. *rhabdodactylus* nov. var.	*Clibanarius signatus* Heller
Ecusson céphalothoracique	avec quatre bandes longitudinales, les médianes, très nettes.	comme dans la forme typique	Les deux bandes médianes plus diffuses se présentent plutôt sous la forme de quatre larges taches dont les deux antérieures sont souvent fusionnées.
Pédoncules oculaires	avec une seule bande très nette, sur la face supérieure.	”	Avec une bande plus claire sur la face supérieure, et une autre sur chaque face latérale.
Chélipèdes	rouges avec les doigts blancs	uniformément rouges	rouge avec des bandes plus claires dessus, dessous et sur les côtés.

Dactyle des pattes ambulatoires	Blanc avec, au plus, des petites taches rouges à la base, dans le prolongement des 5 bandes colorées du propode.	avec cinq bandes colorées sur toute sa longueur dans le prolongement de celles du propode.	comme chez *C. zebra* var. *rhabdodactylus*

Genre *Calcinus* Dana

Calcinus elegans (H. Milne-Edwards 1836)

Pagurus elegans, H. Milne-Edwards, 1836, p. 278, pl. XIII, fig. 2.

"*Calcinus elegans* H. Milne-Edwards", Dana, 1952, p. 458, pl. XXVIII, fig. 10 *a-c.*

Hikuéru, 6 sp.; Takumé, 7 sp.; Tahiti, de nombreux spécimens, dont plusieurs ♀ ovigères. L.c. 4 à 17 mm.

Calcinus gaimardii (H. Milne-Edwards 1848)

Pagurus gaimardii, H. Milne-Edwards, 1848, p. 63.

"*Calcinus gaimardii* H. Milne-Edwards" Dana, 1852, p. 457, pl. XXVIII, fig. 9.

Tahiti, 1 ♂ L.c. 14 mm, dans *Turbo setosus* Gmel.

Calcinus herbstii de Man 1888

"*Pagurus tibicen* Herbst", H. Milne-Edwards, 1836, p. 278.

Calcinus herbstii, de Man, 1888, p. 437.

"*Calcinus herbstii* de Man" (pars), Nobili, 1907, p. 368.

"*Calcinus herbstii* de Man", Forest, 1951, p. 84, fig. 2, 5, 6, 9.

Hikuéru, Tahiti, Takumé: de très nombreux spécimens dont des ♀ ovigères. L.c. 1,5 à 25 mm.

Calcinus latens (Randall 1839)

Pagurus latens, Randall, 1839, p. 135.

Pagurus cristimanus, H. Milne-Edwards, 1848, p. 64.

"*Calcinus latens* (Randall)", Dana, 1852, p. 459, pl. XXVIII, fig. 11.

Calcinus terrae-reginae, Haswell, 1882, p. 158.

"*Calcinus latens* Rand", Nobili, 1907, p. 369.

"*Calcinus terrae-reginae* Haswell", Nobili, 1907, p. 369.

"*Calcinus latens* Randall", Forest, 1951, p. 94, fig. 14-18.

Hikuéru: 7 sp.; Tahiti et Takumé, de très nombreux spécimens dont des ♀ ovigères, L.c. 2 à 11 mm.

Calcinus seurati Forest 1951.

Calcinus seurati Forest, 1951, p. 84, fig. 1, 3, 4, 7, 8.

Tahiti: 3 sp.; Takumé: 5 sp.; Hikuéru: de nombreux spécimens dont beaucoup de ♀ ovigères: L.c. 1,5 à 14 mm.

Remarques.—Cette espèce a été décrite en 1951, d'après des spécimens *récoltés* par Seurat aux Iles Gambier il y a cinquante ans et confondus avec *C. herbstii* par Nobili. Elle est abondamment représentée dans le matériel rassemblé par M. Ranson et surtout parmi les récoltes de Hikuéru. Les marques colorées sur les pattes ambulatoires sont celles que j'avais décrites d'après des spécimens en alcool depuis de nombreuses années, elles varient encore du rouge-orange au brun foncé. Les mesures effectuées confirment qu'il s'agit d'une espèce dont la taille moyenne est sensiblement inférieure à celle de *C. herbstii.* Les plus petites ♀ ovigères ont une carapace longue de 5 mm.

Genre *Pagurus* Fabricius

Pagurus deformis H. Milne-Edwards 1836

Pagurus deformis H. Milne-Edwards, 1836, p. 272, pl. XIV, fig. 2
"*Pagurus deformis* Edw.", Nobili, 1907, p. 370.

Hikuéru: 1 ♂, L.c. 25 mm; Tahiti: 5 ♂, L.c. 17 à 38 mm; 5 ♀ L.c. 11,5 à 16 mm; 5 ♀ ovigères, L.c. 23 à 35 mm; 1 juv. L.c. 4 mm. Dans *Melanella cumingi* (Sow.), *Polynices melanostoma* (Gmel.), Thais pica (Blainville), *Turbo setosus* Gmel.

Pagurus gemmatus H. Milne-Edwards 1848

Pagurus gemmatus, H. Milne-Edwards, 1848, p. 60.
Neopagurus sp., Kamalaveni, 1950, p. 85.

Tahiti: 1 ♂ L.c. 48 mm, 1 ♀ L.c. 18 mm, 1 ♀ ovigère, L.c. 39 mm, 1 ♂ juv. L.c. 9 mm. Dans *Nerita maculata* Pease, *Turbo setosus* Gmel.

Remarques.—Le type de *Pagurus gemmatus* est un très grand ♂ à carapace de 60 mm; les spécimens de Tahiti énumérés ci-dessus appartiennent certainement à cette espèce qui possède des pédoncules oculaires particulièrement courts, et qui est fort proche du *Pagurus asper* de Haan. La seule différence importante réside dans l'ornementation du chélipède gauche dont la face externe de la main est entièrement recouverte de tubercules émoussés chez le *P. gemmatus,* alors que la moitié inférieure de cette région est parfaitement lisse chez *P. asper.* Il est possible que la femelle figurée par Alcock sous le nom de *P. dearmatus* Henderson soit en réalité un *P. gemmatus.* En effet le type de *P. dearmatus* que j'ai examiné au British Museum, une petite ♀ ovigère, possède un chélipède gauche bien plus allongé que le spécimen représenté par Alcock. Le spécimen ♂ des "Mers du Sud" décrit par S. Kamalaveni sous le nom de *Neopagurus* sp. me paraît également être un *Pagurus gemmatus.* Le comparant à cette dernière espèce l'auteur écrit "It differs from *Pagurus gemmatus* M. Edw. in lacking the strong crenulated crest on the propodite of the third leg and in having two spurs on the abdomen." Or *Pagurus gemmatus* ne présente pas de crête sur la troisième patte gauche et possède bien les deux "éperons" (spurs). J'indiquerai ici que je ne considère pas comme valable le genre *Neopagurus* que Miss Kamalaveni caractérise par la présence sur l'abdomen, au niveau de l'avant dernier plépode impair, de ces deux "éperons", au lieu d'un seul. Je ne pense pas que le dédoublement de ce diverticule enigmatique,–qui correspond peut-être à la saillie abdominale "columellaire" de beaucoup de Pagurides–qui n'est pas visible chez les jeunes, et qui est plus développé chez les femelles que chez les mâles, justifie une division du genre *Pagurus,* fort homogène par tout un ensemble de caractères beaucoup plus significatifs (Forest, 1952, p. 32). Si on admettait la validité du nouveau genre il faudrait y rattacher un certain nombre d'espèces: *Pagurus asper* de Haan, *P. gemmatus* H. Milne-Edw. *P. varipes* Heller, etc... Quant à *P. deformis* H. Milne-Edwards, il appartiendrait au nouveau genre par les femelles seulement, les mâles ne possédant qu'un diverticule abdominal simple. Quant à la description de *Neopagurus horai* Kamalaveni, elle me semble applicable à *Pagurus asper* de Haan.

Pagurus megistos (Herbst 1804)

Cancer megistos, Herbst, 1804, p. 23, pl. LXI, Fig. 1.
Pagurus punctualatus, Oliver, 1811, p. 641.
Pagurus spinimanus, H. Milne-Edwards, 1848, p. 61.
"*Pagurus punctulatus* Oliv.", Nobili, 1907, p. 370.

Tahiti: 6 ♂ de 18 à 71 mm; 2 ♀ de 35 et 38 mm; dans *Conus textile* L. (le plus jeune ♂), *Turbo setosus* Gmel.

Remarques.–Le *Pagurus spinimanus* de H. Milne-Edwards dont un spécimen, probablement le type, figure dans les collections du Museum, ne me paraît pas différent de l'espèce qui a surtout été signalée sous le nom de *P. punctulatus* Olivier, mais qui est certainement identique au *Cancer megistos* de Herbst. Il ne faut pas tenir compte de l'abdomen fantaisiste attribué par Herbst à cette espèce: la partie antèrieure du corps est assez précisément figurée pour que le doute ne soit pas possible. Le plus petit spécimen, logé dans un *Conus, présente* un fort aplatissement dorso-ventral.

Pagurus sanguinolentus Quoy et Gaimard 1824

Pagurus sanguinolentus, Quoy et Gaimard, 1824, p. 532, pl. LXXIX, fig. 2.
Pagurus affins, H. Milne-Edwards, 1836, p. 274.
Pagurus euopsis, Dana, 1852, p. 452, pl. XXVIII, fig. 6 *a-c.*
Pagurus depressus, Heller, 1861, p. 248.
"*Pagurus euopsis* Dana", Nobili, 1907, p. 370.

Hikuéru: 2 ♀ de 23 et 26 mm; Tahiti: 1 ♂ de 8 mm; dans *Conus rattus* Hwass, *Pterocera bryonia* (Gmel.); *Turbo setosus* Gmel.

Remarques.—Cette espèce a fréquemment été signalée sous les noms de *Pagurus euopsis* Dana ou de *P. depressus* Heller que l'on a longtemps hésité à considérer comme synonymes: des publications récentes font encore état d'une variété *depressus*, distincte du *P. euopsis* typique. En fait je crois que l'on peut tout au plus parler d'une "forme" *depressus* que présentent les *P. euopsis* ayant vécu dans une coquille à ouverture particulièrement étroite (*Conus* par exemple) sans que cela implique des différences génotypiques (cf. Forest, 1952, p. 35). La comparaison de nombreux spécimens de *P. euopsis* à des types conservés au Museum de Paris m'a amené à la conclusion que l'espèce de Dana avait été précédemment décrite par H. Milne-Edwards (1836) sous le nom de *Pagurus affinis*, et avant lui par Quoy et Gaimard (1824) sous celui de *P. sanguinolentus*. Le type de *P. sanguinolentus*, récolté au cours du Voyage de l'Uranie à l'Ile Maurice (localité douteuse d'après les auteurs est une femelle en assez bon état, à carapace de 26 mm. Les marques colorées ont complétement disparu, mais elle est identique aux *P. euopsis* que j'ai examinés, par tout un ensemble de caractères: forme des pédoncules oculaires, articles du flagelle antennaire présentant la hernie caractéristique signalée par Dana et donnant à la moitié distale de ce flagelle un aspect en dents de scie, forme et ornementation des chélipèdes et des pattes ambulatoires, pilosité. Les pédoncules oculaires sont assez courts chez le type, mais le rapport de leur longueur à la langeur du bord frontal, calculé pour de nombreux, *P. euopsis* adultes, varie dans des proportions considérables, de 1 à 1,5. Les proportions et l'ornementation du propode de la seconde patte ambulatoire gauche (*p.* 3) sont également fort variables. La face externe de cet article est, en général, très élargie (de deux à deux fois et demie plus longue que haute), marquée par une dépression longitudinale, et couverte d'épines cornées longues et aigües et de longs poils raides qui existent aussi sur les trois derniers articles des chélipèdes et des autres pattes ambulatoires. Mais dans d'autres cas, le propode de cette patte est plus allongé, sa face externe non plus déprimée, mais plane ou même convexe et les épines et les poils sont beaucoup moins nombreux. La limite extrême de cette variation est représentée par le type du *Pagurus affinis* de H. Milne-Edwards, un ♂ à carapace de 23 mm, provenant de Ceylan, et par deux autres *P. euopsis* ♂ de la collection, chez lesquels il n'y a plus que de toutes petites épines dans le voisinage du bord supérieur de l'article, et des poils beaucoup moins abondants. Chez ces spécimens on peut considérer, que la seconde patte ambulatoire gauche n'est plus modifiée, mais au contraire de même type que les trois autres. Il existe d'ailleurs des intermédiaires entre la forme typique et cette forme que l'on pourrait qualifier *d'affinis*. Tous les autres caractères, et la coloration en particulier, qui est exactement la même dans tous les cas, montrent qu'il s'agit d'une seule et même espèce. Il faut noter ici que de Man considérait déjà *P. affinis* comme identique à *P. euopsis*.

Pagurus scutellatus H. Milne-Edwards 1848

Pagurus scutellatus, H. Milne-Edwards, 1848, p. 62.

Pagurus fabimanus, Dana, 1851, p. 270, et 1852, p. 454, pl. XXVIII fig. 7 *a-e*.

"Dardanus fabimanus (Dana)", Buitendijk, 1937, p. 273, fig. 18 et 19.

"Dardanus scutellatus (H. M.-Edw.)", ibid., p. 273, fig. 16 et 17.

Tahiti 1 ♂ juv. L.c. 4 mm (sans coquille)

Remarques.—Le type de *Pagurus scutellatus* est un ♂ à carapace de 22 mm, dont la troisième patte thoracique gauche ainsi que le propode et le dactyle de la troisième patte droite manquent. La description et les dessins de *Pagurus fabimanus* donnés par Dana s'appliquent fort bien à ce spécimen dont l'écusson céphalothoracique et les appendices céphaliques ont été figurés par Bouvier (1915, p. 33, fig. 14). Par contre on peut relever dans la texte de H. Milne-Edwards quelques lignes qui expliquent que l'on n'aît pas songé à mettre les deux espèces en synonymie. Il écrit entre autre: "...pince gauche... courte et pointue. Pattes ambulatoires toutes arrondies..." Or, le propode du chélipède gauche est au contraire oblong comme l'écrit Dana à propos de celui de *P. fabimanus*, et si, comme il est probable, la troisième patte thoracique manquait déjà lorsque Milne-Edwards rédigea sa description, ce qu'il dit des pattes ambulatoires ne s'applique en fait qu'à la première paire. Les caractères essentiels sur lesquels repose l'identification des deux espèces sont les suivants: Brièveté de l'écusson céphalothoracique qui contrairement à ce qu'on observe chez les autres *Pagurus*, est nettement plus large que long, pédoncules oculaires longs et en massue, ressemblant à ceux de *P. sanguinolentus*, propode du chélipède droit oblong, infléchi, à bord inférieur en carène aigüe, à face externe couverte de fines spinules dissimulées par une courte pubescence. A. Buitendijk a distingué *P. fabimanus* de *P. scutellatus* d'après l'ornementation du chélipède et de la troisième patte thoracique gauche, appendices qu'elle a figurés dans les deux cas, mais, par la main gauche, le type de *P. scutellatus* me paraît bien plus proche de ce qu'elle présente sous le nom de *P. fabimanus*. Les différences qu'elle relève me semblent seulement d'ordre individuel, le spécimen dénomé *P. scutellatus* n'ayant, en somme, que des épines un peu plus fortes sur le chélipède et des stries un peu plus marquées sur le propode de la *p* 3 gauche que le *P. fabimanus* typique.

Genre *Aniculus* Dana

Aniculus aniculus (Fabricius 1787)

Pagurus aniculus, Fabricius, 1787.
Aniculus typicus, Dana, 1852, p. 461, pl. XXIX, fig. 1.
"*Aniculus aniculus* (Fabr.)", Nobili, 1907, p. 371.

Hikuéru: 2 ♂, L.c. 26 et 29 mm, 1 ♀ ovigère, L.c. 42 mm; Tahiti: 2 ♂, L.c. 29 et 39 mm, 1 ♀, L.c. 14 mm; dans *Turbo setosus* Gmel.

EUPAGURINA Ortmann

Genre *Eupagurus* Brandt

Eupagurus anceps sp. nov.

Hikuéru: 18 ♂, L.c. 1,2 à 3 mm; 5 ♀, L.c. 1,2 à 2 mm, dont 2 ovigères de 1,8 et 2 mm (Syntypes); 17 ♂ et 2 ♀ dont une ovigère, L.c. 1,4 à 3 mm; Tahiti: 3 ♂, L.c. 1,3 à 1,8 mm; 2 ♀, L.c. 1,2 et 1,8 mm Dans *Cerithium nesioticum* Pilsbry et Vanetta, *C. piperitum* Sow. *Planaxis lineolatus* Gould.

Description.—Ecusson céphalothoracique un peu plus long que large. Rostre large, acuminé, proéminent; dentslatérales du bord frontal beaucoup moins saillantes et situées bien plus près des angles antéro-latéraux que de la ligne médiane. Pédoncules oculaires cylindriques, à peu près trois fois plus longs que larges, trapus, le rapport de leur longueur à celle de l'écusson céphalothoracique sensiblement égal à 5/7 chez les adultes. Cornées grandes, non échancrées postérieurement. Ecailles oculaires larges, arrondies, présentant une petite pointe distale insérée par dessous. Pédoncules antennulaires dépassant les cornées de la moitié de la longueur de leur dernier article. Pédoncules antennaires un peu plus longs que les pédoncules oculaires. Ecailles antennaires sub-cylindriques atteignant le quart proximal du dernier article pédonculaire.

Chélipède droit présentant un important dimorphisme sexuel: chez le mâle adulte, propode à peu près de même longueur que la carapace; main assymétrique, avec un bord droit rectiligne ou légèrement concave et un bord gauche fortement convexe; bord interne du doigt fixe très oblique par rapport à l'axe longitudinal de la main. Région antérieure des doigts recourbée vers le bas. Chez la femelle, main à peine plus longue que la région antérieure du céphalothorax, ses bords latéraux régulièrement convexes, le bord interne du doigt fixe dans l'axe longitudinal de la main. Chélipède gauche à peu près de même type dans les deux sexes, ressemblant au chélipède droit de la femelle mais plus petit, le propode ayant une longueur sensiblement égale aux 4/5 de celle de l'écusson céphalothoracique. Chélipèdes très finement granulés chez les mâles adultes. Chez les femelles les granules ont tendance à devenir spiniformes sur les bords de la main. Chez les jeunes, le carpe du chélipède gauche présente une rangée longitudinale de denticules sur la face supérieure, et il existe des tubercules spiniformes disposés en plusieurs rangées longitudinales sur la région palmaire.

Pattes ambulatoires peu déprimées latéralement, dactyle et propode sub-égaux; ongle long, crochu, et acéré, suivi de cinq ou six spinules cornées insérées sous le dactyle; sous le bord inférieur du propode, une petite épine cornée distale, suivie d'une ou de plusieurs spinules très petites.

Coxae de la cinquième paire thoracique dissymétriques, la gauche normale, avec l'orifice génital s'ouvrant vers le bas et bordé postérieurement par une frange de soie dont la longueur n'excède pas son diamètre, la droite plus grosse, présentant du côté interne un renflement au sommet duquel est situé le pore génital obliquement orienté vers le plan sagittal et la région abdominale de l'animal; de très longues soies sinsèrent sur le bord postérieur de l'orifice, barrant transversalement le thorax et viennent recouvrir la coxa gauche.

Quatre pléopodes biramés (pl. 2 à pl. 5) sur le côté gauche de l'abdomen chez la femelle. Trois pléopodes biramés, plus petits (pl. 3 à pl. 5) chez le mâle.

Pilosité faible. Des taches rouge-orangé sur la carapace et les pédoncules oculaires et antennaires, sur les chélipèdes et sur les pattes ambulatoires.

Remarques.—Cette espèce appartient au sous-genre *Pagurixus* créé par Melin pour *P. boninensis* sp. nov. en 1939, par la conformation des coxae de la cinquième paire de pattes thoraciques (Melin, 1939, p. 39, fig. 18) et par la présence de trois pléopodes biramés chez le mâle. Le genre *Eupagurus* manque certainement d'homogénéité: on y a introduit tous les *Eupagurinae* dépourvus de pléopodes pairs dans les deux sexes et de tubes sexuels chez le mâle, et il sera certainement nécessaire, au cours d'une révision générale, de le sub-diviser en plusieurs groupes qui auront une valeur générique et non pas seulement sub-générique. Si les orifices mâles sont disposés de la même facon chez *Eupagurus anceps* sp. nov. et chez *E. boninensis,* il ne semble pas cependant que l'on ait affaire à une même espèce. La comparaison est rendue difficile par le fait que nous ne connaissons la seconde que par la description d'un seul exemplaire mâle, privé de ses deux chélipèdes. Les caractères figurés par Melin, en particulier la forme du bord frontal, des pédoncules et des écailles oculaires, ainsi que les particularités des antennules, rendent improbable l'identité des deux espèces.

Eupagurus maorus, décrit de Tahiti par Nobili, est connu par une seule femelle, en mauvais état, conservée au Museum. Ce spécimen est bien plus grand que les *E. anceps* puisqu'il mesure 6 mm (L.c.). La forme de la région antérieure de la carapace, les proportions des appendices céphaliques et des deux derniers articles des pattes ambulatoires, la coloration sont différentes chez les petits *Eupagurus* récoltés par M. Ranson et chez *E. maorus,* mais ces différences pourraient être liées à la taille plus grande de ce dernier. Par contre les chélipèdes sont très grêles et portent des rangées de tubercules fort saillants chez *E. maorus* alors que, chez *E. anceps,* ces appendices sont assez trapus et ont une face supérieure presque lisse. Il est regrettable que l'espèce de Nobili ne soit encore connue que par une femelle ce qui rend incomplète toute comparaison avec une forme comme *Eupagurus anceps,* dont le dimorphisme sexuel est aussi net et aussi frappant: la pince gauche du mâle est ici beaucoup plus volumineuse que celle de la femelle et de forme bien différente, à tel point que les deux sexes paraissent à première vue appartenir à des espèces différentes.

En ce qui concerne *E. maorus,* il est possible qu'on soit amené à le mettre en synonymie avec *E. laevimanus* Ortmann qui a été décrit d'après un seul spécimen ♂ à carapace de 6,5 mm environ. Les différences indiquées par Nobili portent à peu près uniquement sur l'ornementation du chélipède droit, complètement lisse chez *E. laevimanus.* N'est-on pas ici encore en présence d'un cas de dimorphisme sexuel? Il serait nécessaire, pour répondre à la question, d'examiner le type d'Ortmann, et de disposer de plusieurs spécimens mâles et femelles d'une même localité.

Eupagurus anceps est l'une des plus petites espèces de pagures décrites. Les plus grands individus mâles ont une carapace de 3 mm; ceux dont la carapace ne mesure que 2 mm ont déjà, le plus souvent, un chélipède droit de forme caractéristique. Chez les plus petits, mais aussi, il faut le noter, chez quelques individus parmi les plus grands, cet appendice diffère peu de celui des femelles. Il est probable que le dimorphisme apparaît à un certain stade du développement sexuel, lequel peut n'être pas étroitement lié à l'accroissement de taille. Les femelles ont une taille maximum de 2 mm (L.c.), la plus petite ovigère mesure 1,6 mm (L.c.). Il y a 10 à 14 oeufs, énormes par rapport à la taille de la mère, puisque leur diamètre est compris entre 400 et 500μ. Ces oeufs sont disposés le long de l'abdomen en un double cordon.

Catapaguroides? trichophthalmus sp. nov.

Tahiti: 1 ♂ L.c.; 3 mm (Holotype), *p* 1 gauche, *p* 3 droit et les 2 *p* 4 manquent.

Description.—Largeur de l'écusson céphalothoracique légèrement supérieure à sa longueur, celle-ci représentant les 3/5 environ de la longeur totale de la carapace. Rostre acuminé, très proéminent, dépassant légèrement le milieu des écailles oculaires. Pédoncules oculaires extrèmement trapus, élargis au niveau du tiers proximal, le diamètre à ce niveau compris deux fois environ dans la longueur qui est égale aux 3/5 de celle de l'écusson céphalothoracique. Cornées paraissant légèrement invaginées, leur bord antérieur atteignant l'extrémité antérieure de l'avant-dernier article des pédoncules antennulaires et dépassant le milieu du dernier article des pédoncules antennaires. Ecaille antennaire longue et sub-cylindrique, arrivant au tiers distal du dernier article lorsqu'on la rabat contre le pédoncule.

Chélipède gauche manquant, un peu plus petit que le droit d'après la taille des coxae. Chélipède droit très allongé avec le merus relativement court, carpe aussi long que la carapace; longueur du propode égale à deux fois et demie celle de l'écusson céphalothoracique. Doigts à ongles non cornés légèrement recourbés vers le bas et représentant moins du tiers de la longueur totale de la main. Tous les articles lisses ou très finement granuleux; sur le merus deux dents, l'une médiane, l'autre sub-distale, au bord inférieur de la face interne, et une dent subdistale au bord inférieur de la face externe.

Pattes ambulatoires de la première paire nettement plus courtes que le chélipède droit. Dactyle et propode peu déprimés latéralement et subégaux, le premier avec 8 ou 9 épines cornées longues et fines sur le bord inférieur, en arrière de l'ongle, le second avec 3 ou 4 épines plus espacées sur ce bord. Deuxième patte ambulatoire droite manquant. *p* 3 gauche un peu plus longue que la précédente mais de même type, avec 11 épines sous le dactyle, et 4 sous le propode. Quatrièmes pattes thoraciques manquant. Cinquièmes pattes se terminant par une très courte pince. Coxa droite pourvue d'un long tube sexuel rabattu contre le flanc droit et dont la région distale, plus mince, est légèrement spiralée. Orifice sexual gauche surmonté d'une petite papille conique.

3 plépodes impairs non ramifiés (pl. 3 à pl. 5).

Telson allongé, dissymétrique; sur le bord des deux lobes postérieurs, de part et d'autre de l'encoche médiane, quelques denticules et, en avant, de très longues soies.

Pilosité forte, constituée par de longs poils très fins, transparents, raides, particulièrement nombreux et développés sur les pédoncules oculaires, en arrière des cornées, sur les écailles antennaires, et sur le dessus des chélipèdes et des autres pattes thoraciques.

Onze paires de branchies bi-sériées. Les lamelles situées près de l'insertion de chaque branchie profondément échancrées au sommet, mais l'échancrure diminuant puis disparaissant progressivement quand on se rapproche de l'extrémité.

Remarques.—Ce n'est qu'après de longues hésitations que j'ai rattaché cette petite espèce au genre *Catapaguroides* A. Milne-Edwards et E. L. Bouvier, d'autant plus que la femelle est encore inconnue. Les *Eupagurinae* comptent plusieurs genres chez lesquels les mâles possèdent un long tube sexuel à droite alors que le gauche est beaucoup plus court ou inexistant. Ce sont, en plus des *Catapaguroides*, auxquels on doit probablement rattacher les *Cestopagurus* Bouvier, le *Catapagurus* A. Milne-Edwards, les *Paguroides* Henderson, et les *Nematopagurus* A. Milne-Edwards et E. L. Bouvier, La présence d'appendices pairs sur le premier segment abdominal de la femelle sépare ces derniers des autres genres, et ceux-ci sont habituellement distingués les uns des autres par la position du tube sexuel droit et par la forme des feuillets branchiaux. Le mâle décrit ici est bien pourvu d'un tube sexuel droit qui remonte le long du flanc droit comme chez *Catapagurus* et *Pagurodes* au lieu d'être dirigé vers la gauche comme dans les autres genres. Par contre ses branchies ne sont pas quadri-sériées comme chez *Pagurodes*, ni simplement bisériées comme chez *Catapagurus* et *Nematopagurus*. Elles sont de même type que chez *Catapaguroides*, avec pour une même branchiet tous les intermédiaires entre les lamelles profondément bilobées et les lamelles entières.

Par la forme du bord frontal, des pédoncules oculaires, des chélipèdes et des pattes ambulatoires, le spécimen de Tahiti est bien éloigné des *Catapagurus* et des *Nematopagurus*. La réduction des pédoncules oculaires s'observe chez *Pagurodes*, mais c'est chez *Catapaguroides* que l'on trouve le plus de variété dans le développement de ces appendices, comme en témoignent les noms attribués à plusieurs espèces: *microps, megalops, macrophthalmus*. C'est dans ce genre que l'on trouve également des formes à rostre très proéminent, à pattes ambulatoires à dactyles relativement courts. L'une d'entre elles, *C. iris* Bouvier des Acores, possède un chélipède droit qui par la forme et les dimensions, ressemble à celui décrit ci-dessus. Le type des feuillets branchiaux, la présence d'un court tube sexuel à gauche, quelques ressemblances ou plutôt des différences moindres dans certains appendices, pédoncules oculaires, chélipèdes, pattes ambulatoires, m'ont paru, au total, plus importants que l'orientation du tube sexuel droit, qui est celle des *Catapagurus*. C'est finalement sous le nom générique de *Catapaguroides* que l'espèce a été décrite. Il va de soi que ce choix n'est pas définitif. Il sera confirmé ou infirmé lorsqu'on connaîtra la femelle et surtout lorsque les *Eupagurinae* auront été revisés: les difficultés rencontrées ici montrent une fois de plus l'insuffisance des caractères retenus jusqu'à maintenant pour distinguer les différents genres. En l'absence d'une meilleure caractérisation de chacun d'eux, on risque d'être amené à en créer inutilement de nouveau ou à placer côte à côte des espèces phylogénétiquement éloignées.

Catapaguroides? trichophthalmus a été récolté dans la zône intercotidale et on peut ainsi le rapprocher de *C.* (*Cestopagurus*) *coutieri* Bouvier des récifs madréporiques de Djibouti et de *C. timidus* (Roux), espèce méditerranéenne que l'on trouve depuis la côte jusqu'à une profondeur de 1.200 mètres. La plupart des représentants des genres dont il a été question plus haut sont sub-littoraux ou franchement abyssaux.

Le genre *Catapaguroides* était considéré comme exclusivement atlantique. Si l'on y rattache les *Cestopagurus*, sa répartition s'étend à l'Indo-Pacifiquè, de la Mer Rouge aux Iles Bonin. S'il se confirme que l'espèce décrite ci-dessus est bien un *Catapaguroides*, la limite orientale du genre se verra repoussée jusqu'à Tahiti.

COENOBITIDAE Dana

Genre *Coenobita* Latreille

Coenobita hilgendorfi Terao 1913

"Coenobita clypeata Herbst", Latreille, 1826, p. 277.
"Coenobita clypeatus Lat.", Nobili, 1907, p. 373.
Coenobita hilgendorfi (*nom. nov.*) Terao, 1913, p. 388.

Hikuéru: de nombreux spécimens, L.c. 18 à 44 mm, comprenant des ♀ ocigères; Tahiti: 1 ♂ L.c. 35 mm; tous dans *Turbo setosus* Gmel.

Coenobita perlatus H. Milne-Edwards 1837

Cocnobita perlata, H. Milne-Edwards, 1837. p. 242.
"Coenobita rugosus Edw." (*pars*) *"Coenobita rugosus* var. *granulosa* (sic) Bouvier" et *Coenobita perlatus* Edw.", Nobili, 1907, p. 373.

Hikuéru et Takumé: très nombreux ♂ et ♀, L.c. 2 à 43 mm.

Remarques.—La révision des Cénobites effectuée par Bouvier (1889-90) ne me paraît pas entièrement satisfaisante. Il s'agit d'un groupe où la variabilité individuelle est grande, et où la création de plusieurs variétés a entraîné une certaine confusion. Je crois par exemple que le *Coenobita compressus* de Guérin est distinct du *C. rugosus* de Milne-Edwards; il est possible qui ces deux espèces aient des aires de distribution différentes, la première, dont le type a été récolté à Payta (Pérou) étant cinfinée au Pacifique oriental. D'autre part, je considère que les *Coenobita rugosus var. granulatus* Bouvier signalés aux Iles Gambier par Nobili, sont en réalité des *C. perlatus.* Je n'ai pas trouvé isi le type de la variété de Bouvier, mais des spécimens déterminés par cet auteur qui me paraissent également identifiables à *C. perlatus.* La confusion a probablement sa source dans le caractère principal proposé pour séparer *perlatus* de *rugosus:* présence d'un tube sexuel sur la coxa de la dernière patte thoracique droite, beaucoup plus long dans la première espèce que dans la seconde. Or si ce caractère permet de distinguer les individus de grande taille, il est inutilisable pour les autres, car les jeunes *C. perlatus* ♂ ne se distinguent guère des *C. rugosus* ♂ à ce point de vue. Chez *C. perlatus* les granulations présentes sur les trois premières paires de pattes sont beaucoup plus fortes et moins nombreuses, et la seconde patte ambulatoire gauche ne possède jamais une face externe plane sur sa plus grande partie, très finement granuleuse, et séparée de la face supérieure par une carène anguleuse comme c'est le cas chez *C. rugosus.* Mais c'est encore la coloration qui permettra souvent de savoir immédiatement à laquelle des deux espèces on a affaire. Dans l'alcool, les grands *C. perlatus* ont une coloration d'ensemble variant entre le jaune-orange et le rouge foncé, plus intense sur les régions proximales du propode et du dactyle des pattes ambulatoires. Les tubercules sont blancs. Les individus plus petits ont une coloration blanchâtre avec des taches colorées persistantes, variant entre le rouge clair et le brun violacé sur la face externe des pattes ambulatoires. Ces taches sont localisées sur le tiers proximal du propode et sur l'articulation propode-dactyle; on les observe chez les plus petits individus. Chez *C. rugosus,* la teinte d'ensemble varie du blanc rosé au gris violacé, les marques colorées sont brunâtres: la plus intense est une large tache sur la face externe de la main gauche. Les spécimens les plus frais présentent également des aires brunes sur la moitié distale du dactyle, sur une grande partie du propode et sur la moitié supérieure du carpe des pattes ambulatoires. *C. merlatus* est de loin l'espèce de Cénobite la plus abondante dans le matérial étudieé. Il faut noter qu'aucun spécimen n'en a été récotlé à Tahiti.

Coenobita rugosus H. Milne-Edwards 1837

Coenobita rugosa H. Milne-Edwards, 1837, p. 241.
"*Coenobita rugosus* Edw." (*pars*), Nobili, 1907, p. 373.

Hikuéru: 7 ♂, L.c. 16 à 27 mm; 3 ♀, L.c. 12 à 25 mm; Tahiti: 1 ♀, L.c. 10 mm; Takumé: 1 ♀, L.c. 16 mm. Dans *Turbo argirostomus* L., *T. setosus* Gmel.

Remarques.—Il a été déjà question de cette espèce dans les remarques relatives à *C. perlatus.* *C. rugosus* paraît beaucoup plus rare, tout au moins aux niveaux où ont été effectuées les récoltes. Il faut aussi noter qu'il s'agit d'individus de taille assez grande (La taille maximum de l'espèce est bien inférieure à celle de *C. perlatus*). Les jeunes sont complétement absents de la collection Ranson.

Genre *Birgus* Leach

Birgus latro (L. 1767)

Cancer latro, Linné, 1767, p. 1.049
Birgus latro, Leach, 1815, p. 337

Niau: 1 ♂, L.c. 140 mm.

APPENDICE

Coquilles de Gasteropodes Habitees par les sept Especes de Paguridea Representees par de Nombreux Specimens.

	Clibanarius corallinus	*C. humilis*	*Calcinus elegans*	*C. herbstii*	*C. latens*	*C. scurati*	*Coenobita perlatus*
Aspella anceps (Lmk.)	+						
Astraea confragosa (Gould)	+						+
Bullaria punctulata (A. Adams)		+			+		
Bursa affinis (Broderip)							+
B. bufonia (Gmel.)	+						
B. cruentata (Sow.)	+						+
B. siphonata (Reeve)	+						+
Cantharus fumosus (Dillw.)		+					
C. undosus (L.)	+	+	+	+	+	+	+
Casmaria vibex (L.)				+			+
Cerithium columna Sow.	+			+	+	+	+
C. mesioticum Pilsbry et Vanetta		+		+	+		
C. patiens Bayle	+	+				+	
C. piperitum Sow.		+			+	+	+
C. rubus (Martyn.)	+		+	+			+
C. sinensis (Gmel.)	+		+	+	+	+	
C. tuberculata L.							+
Charonia distorta (Sch. et Wagner)				+			
Columbella sp.		+			+		
Conus catus Hwass					+		
C. coronatus (Gmel.) Dillwyn					+		
C. lividus Hwass					+		

	Clibanarius corallinus	*C. humilis*	*Calcinus elegans*	*C. herbstii*	*C. latens*	*C. scurati*	*Coenobita perlatus*
C. miliaris Hwass					+		
C. rattus Hwass			+		+		
C. sponsalis Chemnitz					+		
C. tulipa L.	+						+
Coralliophila bulbiformis (Conrad)							+
Cymatium chlorostomum (Lmk.)	+	+		+			+
C. pileare (L.)				+			
C. rubecula L.							+
C. tuberosum (Lmk.)	+	+		+	+		+
Cypraea moneta L.	+		+	+	+		
C. obvelata Lmk.					+		
C. caput serpentis L.			+				
C. ventriculus Lmk.			+				
Drupa aspera (Lmk.)	+						
D. cancellata (Q. et G.)	+			+			+
D. elata (Blainv.)	+				+		+
D. fiscella (Chemn.)	+	+			+		
D. horrida (Lmk.)	+		+				+
D. hystrix (L.)	+		+				+
D. morus (Lmk.)	+			+	+		
D. ochrostoma (Blainv.)				+			
D. ricinus (L.)	+						+
D. speciosa (Dunker)	+						+
D. tuberculata (Blainv.)	+	+					+
Iopas sertum (Brug.)							+
Littorina obesa Sow.						+	+
Melampus fasciatus Desh.		+	+		+		
Melanella cumingi (A. Adams)		+			+		
Mitra astricta Reeve		+			+		
M. litterata Lmk.		+		+		+	

	Clibanarius corallinus	*C. humilis*	*Calcinus elegans*	*C. herbstii*	*C. latens*	*C. seurati*	*Coenobita perlatus*
M. maculosa Reeve	+	+			+		
M. nucea (Gronov.)					+		
M. pontificalis Lmk.					+		
Murex triqueter Born							+
Nassa gaudiosa Hinds				+	+		
Natica marochiensis (Gmel.)		+		+	+		
Nerita maculata Pease		+		+			
N. plicata L.	+			+		+	+
Neritina pisiformis Recluz		+					
N. reticulata Sow.						+	
Peristernia nassatula (Lmk.)	+	+		+			
Planaxis abbreviatus Pease		+					
P. lineolatus Gould		+				+	
Polynices simiae (Desh.)		+					
Strombus floridus Lmk.	+		+	+	+	+	+
S. gibberulus L.				+	+		+
Tectarius bullatus (Martyn)	+						+
Terebra confusa E. A. Smith		+					
T. crenulata (L.)	+						
Thais aculeata (Regenfuss)	+			+			
T. affinis (Reeve)	+		+				+
T. pica (Blainv.)			+	+			
Tritonalia sp.		+					
Turbo argirostomus L.	+		+	+			+
T. petholatus L.							+
T. sétosus Gmel.	+		+	+		+	+
Vasum ceramicum (L.)	+			+	+		+

OBSERVATIONS SUR L'EPOQUE DE LA REPRODUCTION DE *PINCTADA MARGARITIFERA* (L.) ET DE QUELQUES AUTRES ORGANISMES MARINS DANS LES TUAMOTU. LA CAUSE DU NANISME DE *P. MARGARITIFERA* (L.) DANS LE LAGON DE TAKAPOTO

Par Gilbert Ranson

Muséum National d'Histoire Naturelle de Paris, France

Résumé

L'auteur a démontré expérimentalement que les glandes génitales de l'Huître perlière, *Pinctada margaritifera* (L.) ne sont fonctionelles que d'octobre à février, dans les lagons des Tuamotu. Tout le reste de l'année on n'y trouve que des produits génitaux degénérescents, "restes de la saison de reproduction."

L'émission des produits génitaux a lieu en décembre et janvier. Il n'y a pas deux émissions par an. Des milliers de collecteurs artificiels ont été déposés dans les lagons de Hikueru, de juin à novembre.

Seuls ceux de novembre ont capturé des quantités considérables de larves qui s'y sont fixées.

Les Mollusques, les Echinodermes, les Poissons ont été examinés du même point de vue. Il est apparent que leur reproduction n'a lieu également qu'a la même période qui correspond à l'été austral. La température n'augmente que de 3° à 5° C. Mais les vents sont N. W. et c'est la saison des pluies.

C'est une erreur de croire que dans les régions tropicales, les animaux marins reproduisent toute l'année.

Des pêches planctoniques ont été faites de juin à novembre. Le filet fonctionnait pendant un quart d'heure. Le plancton obtenu, étudié, est extrêmement pauvre en larves. Sa masse essentielle est constituée de Chaetognathes, d'Appendiculaires et de Copépodes.

Dans le lagon de Takapoto, par suite d'un isolement assez prononcé de la mer, l'eau a une densité plus élevée: 1030, au lieu de 1025. La température est le même qu'ailleurs. Le plancton y est moins abondant. L'Huître perlière, la même espèce, ici est naine bien que très vivace. C'est la salinité qui en est le facteur déterminant. Son action doit se faire sentir sur l'oeuf même au cours du développement.

J'ai séjourné dans les Iles Tuamotu, en particulier à Hikueru et Takume, de mai à octobre 1952. C'est la période d'hiver. La température de l'air est de 28°–30° (jour), celle de l'eau 26°–28°. D'octobre à mai, c'est l'été. Le service météorologique de l'Ile d'Hikueru m'a donné les températures maxima de 30°–33° (jour.) pour l'air en janvier et février.

J'ai examiné au microscope l'état des glandes génitales de milliers d'Huîtres perlières, *Pinctada margaritifera* (Linné) ainsi que celui d'autres organismes marins: Coelentérés (Coraux), Mollusques, Echinodermes, Crustacés, Poissons. J'ai fait de nombreuses pêches planctoniques. Dans le lagon d'Hikueru, j'ai pu noter qu'en certains endroits, il y a plus de mâles que de femelles, en d'autres c'est l'inverse et enfin ailleurs il y a égalité. Les causes de ces différences n'ont pas été trouvées. C'est un problème tres complexe.

J'ai pu établir d'une manière certaine que de mai à octobre, les glandes génitales de *Pinctada margaritifera* ne sont pas fonctionnelles. Elles sont alors presque entièrement vides de produits génitaux. Ce qu'il en reste est dégénérescent. Les oeufs, déformés, ont leur noyau décentré; leur protoplasme est formé d'amas granuleux anormaux. Je désigne ces produits dégénérescents sous le nom de "restes de la saison de reproduction". Le même phénomène a lieu chez les Ostréidés ou je l'ai bien observé dans la région de Marennes, en France. Toutefois dans les Tuamotu, quelques-uns (très rares), de ces "restes" sont rejetés dans l'eau et des oeufs sont fécondés. En effet j'ai trouvé quelques larves dans le plancton. Le bateau trainait le filet pendant un quart d'heure ce qui représente un volume d'eau, tamisé, considerable. Je n'ai toujours trouvé que quelques larves de Mollusques gastéropodes et lamellibranches. Il est très intéressant de noter que dans ce plancton récolté pendant ces 6 mois de l'année il n'y a pour ainsi dire pas de larves, ni de Mollusques, ni de Crustacés ni de Poissons; sa masse essentielle étant constituée de Chaetognathes, d'Appendiculaires et de Copépodes ou Ostracodes (à Takaroa).

J'ai noté, de la même facon, que les Coraux, tous les Mollusques lamellibranches ou gastéropodes du lagon et de l'extérieur, les Echinodermes, n'étaient pas en état de reproduction.

J'ai déposé dans le lagon d'Hikueru des collecteurs à divers moments, aux cours de cette période. On n'y a pas observé de fixation d'organismes.

C'est en octobre seulement que l'on assiste à la remontée spectaculaire de certains Poissons dans les lagons, par les "passes". J'ai constaté que leurs glandes génitales étaient proches de la maturité. Chez les Mollusques les glandes commencent à être fonctionnelles.

La température de l'eau augmente de 2 degrés par rapport à juillet. Il est possible d'ailleurs que d'autres facteurs que la température, interviennent dans ce phénoméne.

C'est en décembre, janvier et février qu'a lieu la reproduction des Huîtres perlières. J'ai fait déposer dans le lagon d'Hikueru, en novembre 1952, des milliers de collecteurs. A la fin de février 1953 des quantités considérables de jeunes Huîtres y étaient fixées. On m'en a envoyé des échantillons. Ils avaient 2 et 3 mois. C'est là une synthèse expérimentale vraiment démonstrative.

On peut admettre d'après ce que j'ai dit précédemment que pour tous les autres organismes marins de la zone néritique de ces régions, il en est de même.

De décembre à avril il doit y avoir plusieurs émissions de produits génitaux comme on le constate chez les Ostréidés, mais on peut dire que *Pinctada margaritifera* dans les Tuamotu ne présente pas deux périodes de reproduction au cours d'une même année.

D'une manière générale les biologistes ont tendance à croire que dans les regions équatoriales les organismes marins reproduisant toute l'année. C'est une erreur.

Dans le lagon de l'Ile Takapoto, l'Huître perlière n'atteint jamais plus de 8–10 cms de large alors qu'ailleurs elle atteint facilement 15–20–25 cms. Les valves de sa coquille ne sont jamais très épaisses. Ce n'est pas un état pathologique car elle paraît très vivace: sa coquille croit normalement, sans irregularités, sans épaississements. La température de l'eau est la même que dans les autres lagons mais sa salinité est beaucoup plus élevée, 1030 au lieu de 1025. Le lagon de Takapoto a très peu de communications avec la haute mer, l'évaporation est grande. Les plongeurs souffrent de cet excès de salinité, au sortir de l'eau. J'ai fait des prises de plancton en diverses zones du lagon. J'ai constaté sa pauvreté extraordinaire par rapport aux autres lagons pourtant pas très riches à l'epoque de l'année où mes observations ont été faites.

Salinité élevée, plancton pauvre, telles sont les causes du caractère signalé plus haut des Huîtres perlières de Takapoto. Ces Huîtres sont naines. Le nanisme de la coquille de ces Huîtres trouve ainsi son déterminisme parfaitement établi.

On peut comparer le lagon de Takapoto à la Méditerranée par rapport à l'Atlantique. Ce n'est pas la température qui est la cause du nanisme des organismes—sous les mers chauds beaucoup de mollusques sont géants—c'est bien la salinité qui est le facteur determinant—son action peut se faire sentir sur l'oeuf même, au cours de développement.

SUMMARY

Experimentally the author has demonstrated that in the lagoons of the Tuamotu Islands the genital glands of the Pearl Oyster, *Pinctada margaritifera* (L.) are functioning from October till February only. During the remaining part of the year they contain degenerating genital products only, "remains from the season of reproduction."

The discharge of genital products takes place in December and January. There are not two yearly periods of discharge. Thousands of artificial cultchs have been deposited in the lagoons of Nikueru, from June till November. Only those deposited in November became covered with considerable quantities of larvae settled upon them.

The Mollusks, the Echinoderms, the Fishes have been examined from the same point of view. It is apparent that their reproduction also takes place only in the period corresponding with the southern summer. The temperature rises only 3 to 5 degrees, but the winds are N.W. and it is the season of the rains.

It is erroneous to believe that in tropical regions reproduction of the marine animals takes place during the whole year.

Plankton was collected from June till November, the net being towed during a quarter of an hour. The obtained plankton after examination proved to contain extremely few larvae. It essentially consisted of Chaetognathes, Appendicularians, and Copepods.

In the lagoon of Takapoto the water has a greater density (1030 instead of 1025) on account of a rather pronounced isolation from the sea. The temperature is the same in the two regions. The plankton is less abundant in the lagoon. The pearl oyster, the same species, is a dwarf form, though very healthy. The high salinity is the factor determining the small size. The action of the high salinity must manifest itself already on the eggs during development.

November 25, 1953

SYMPOSIUM ON PRODUCTIVITY IN TEMPERATE AND TROPICAL WATERS

Convener: Dr. N. K. **Panikkar**, Central Marine Fisheries Research Station, Mandapam Camp, South India.

Secretary: Mr. **Herminio R. Rabanal**, Bureau of Fisheries, Manila, Philippines.

. . . .

PROCEEDINGS

Dr. N. K. Panikkar convened the symposium at 8:50 A.M. with brief introductory remarks. He mentioned the importance of studies along this field especially in relation to oceanography and he acknowledged the cooperation of the various contributors in sharing their investigation in this symposium. Then he proceeded to set the method of presenting the various papers and the time limit of presentation in order that all the papers may be amply discussed by the scientists in attendance. The papers were so arranged as to start with those dealing with inland or fresh waters, then those on estuarine situations, to be followed by the bulk of papers on marine situations. The last papers dealt on special features on the subject.

Paper No. 1—Kuronuma, K.—Fish Production in Fresh Water Units of Japan. (Communicated by Dr. Y. Okada).

Discussion—Reserved until the two papers on inland waters were both read.

Paper No. 2—Beauchamp, R.S.A.—Herbivorous Animals and the Fertility of Tropical Inland Waters. (Communicated by Dr. A. C. Hardy, U.K.).

Discussion (Paper 1 and 2)

Dr. R. L. **Clarke** (U.S.A.)—Does the writer consider the herbivore as the most important link in the productivity of aquatic habitats?

Mr. H. S. **Swingle** (U.S.A.)—I would consider the role of bacteria on the bottom deposits as more important than the herbivore. It has been shown in pondfish culture that herbivore alone, carnivore alone, or omnivore alone would produce less than if a combination is used. Bluegills alone will produce about 500 pounds per acre. A combination of bluegill and bass will produce about 400 pounds while a combination of bluegills, bass and shad will produce 1000 pounds per acre.

Dr. A. C. **Hardy** (United Kingdom)—I believe that the author did not have the intention to point out one factor as more important, but he merely wanted to convey the importance of one of these factors.

Dr. N. K. **Panikkar** (India)—I quite agree with Dr. Hardy that many factors are important in productivity. For example it has been found that in saline ponds trace elements such as boron and manganese are very important and that sulfates do not seem to be limiting.

Paper No. 3—Ferguson Wood, E. J.—Some Considerations on Estuarine Productivity. (Communicated by Dr. D. J. Rochford, Australia).

Discussion

Dr. J. D. F. **Hardenberg** (Indonesia)—Has this work been done under tropical or temperate conditions?

Dr. D. J. **Rochford** (Australia)—Under temperate conditions.

Paper No. 4—Panikkar, N. K. and R. Jayaraman—Some Aspects of Productivity in Relation to Fisheries of Indian Neritic Waters. (Comunicated by Dr. N. K. Panikkar).

Discussion

Mr. M. **Uda** (Japan)—It might be possible that the eastern or western monsoon along the Indian coast also causes upwelling.

Dr. J. C. **Marr** (U.S.A.)—Have you found whether swarms of dinoflagellates cause mortality to fish?

Dr. J. D. F. **Hardenberg** (Indonesia)—I believe that intense swarms of dinoflagellates, besides other organisms, would cause mortality. One such mortality occurs in the case of Trichodesmium.

Dr. M. J. **Lobell** (FOA, Thailand)—In what type of water do we expect upwelling to occur?

Mr. P. R. **Manacop** (Philippines)—In that connection I wish to cite an instance of a certain area in northern Mindanao where a concentration of plankton occurs during April and May. This concentration attracts whales and devil fishes possibly caused by upwelling in this region at this period.

Dr. M. W. **Johnson** (U.S.A.)—It is a well known fact that the return of nutrients to the water is easier to get in shallow water.

Dr. N. K. **Panikkar**—That is quite true as the physical disturbances occur from surface to the bottom in such waters.

Dr. M. J. **Lobell**—What is the source of what you referred to in your paper as "mud banks"?

Dr. N. K. **Panikkar**—The definite source of mud banks is still a subject of controversy. There are two theories advanced:

a. They are caused by laterites from inland carried down due to excessive rainfall.

b. They are caused by rising ooze from the sea bottom after heavy rainfall.

Dr. D. J. Rochford—Is this a part of the regular cycle of the water in the region?

Dr. N. K. Panikkar—It seems that it is.

Mr. P. R. Manacop—Is this area a place of regular trawling operation?

Dr. N. K. Panikkar—No, trawling is done in a different region. This place is virgin.

Dr. Y. Hiyama (Japan)—It is quite difficult to understand why the eastern coast of India cannot be as productive as the western coast. Do you suppose that it may be due to some economic factors obtaining in these places?

Dr. N. K. Panikkar—I do not believe so. These figures, however, are taken far apart in the sea based on units per mile per run.

Dr. J. D. F. Hardenberg—Yes, the comparative productivity is quite hard to reconcile with the presence of big rivers draining in the eastern side.

Dr. N. K. Panikkar—That is quite understandable because these figures have to do with figures for sea fisheries alone, without production from estuarine situations.

Dr. D. J. Rochford—Do you have data on phosphate during the year especially in relation to the appearance of the so-called "mud banks"?

Dr. N. K. Panikkar—Yes, but our data on these are not quite complete.

Dr. M. J. Lobell—What is the nature of the prevailing winds along this coast?

Dr. N. K. Panikkar—The prevailing winds consist of rainy south west monsoon and dry northeast winds.

Dr. G. L. Clarke—Is the upwelling caused by offshore or inshore winds?

Mr. M. Uda—In that connection is not the circulation in Bengal Bay cyclonic?

Dr. A. C. Hardy—Strong winds blowing shoreward bring in the surface waters to the shore. The temporary rise causes a returning undercurrent which rises again with the nutrients when blown inward after reaching some distance from the shore.

Mr. P. R. Manacop—The fact that the catch in deeper waters is less than in shallower waters supports that contention. In trawling, most production is within 5 to 10 fathoms.

Dr. M. J. Lobell—Is there any thermocline in these waters?

Dr. N. K. Panikkar—We have not investigated that aspect.

Mr. M. Uda—It is possible that the existing conditions in these areas explain the spawning ground for mackerel.

Dr. W. A. Clemens (Canada)—In the area along the coast of Burma and Malaya, what is the nature compared with the Indian coast?

Dr. N. K. Panikkar—We have no data for those places.

Dr. R. W. Hiatt (Hawaii)—Does the molluscan fauna in this region follow the abundance of the fish as a fishery?

Dr. N. K. Panikkar—Mollusca fisheries are better in the east coast; shrimp fisheries better in the west coast. Fish culture is better and more developed in the east coast. Here there is no sudden change of salinity from the estuaries to the coast.

Paper No. 5—Huntsman, A. G.—Factors for Fish Productivity. (Communicated by Dr. W. A. Clemens).

Discussion

Dr. C. Miles (IPFC-FAO)—Present evidences tend to refute the generally accepted finding that higher productivity is found in higher latitudes (temperate areas) and lower productivity in lower latitudes (equatorial belts), but these may appear to be just a few local and exceptional cases. This has been explained with the rapid metabolic turnover in the tropical zones. However, in the case of fresh water the inverse is true with regard to the generalization with latitude. The main setback in the inland waters in higher latitudes is light, which cannot be continuously utilized; whereas in tropical fresh waters this supply is continuous and with constant supply of the necessary nutrients, metabolic activity or organic production proceeds. An innovation which has in some way replenished the nutrient supply in tropical inland waters is the use made of night soil. This practice is becoming of general adoption in many countries of the Indo-Pacific Region.

Mr. H. S. Swingle.—The main difficulty in temperate countries is that in deeper waters productivity is only possible during summer. I believe it could not be doubted that productivity in fresh water ponds could greatly be increased mainly through feeding, up to certain limit, but the high cost of feed has to be considered. Cheaper ways of obtaining fish food has been utilized as in the case now of fertilization of ponds.

Dr. A. C. Hardy—In the cold polar waters the bottom fauna are richer than in the tropics. Whales for example graze in these waters.

Dr. Y. Hiyama—There are so many factors involved that may modify production in fresh-water.

Dr. M. J. Lobell—From the ideas expressed I believe it would not be safe to use the much modified productivity in inland waters as basis of comparison.

Paper No. 6—Wimpenny, R. S.—The Productivity of Temperate and Tropical Waters. (Communicated by Dr. A. C. Hardy).

Discussion

Dr. G. L. **Clarke**—If the metabolic rate in fish is uniformly rapid in warm waters, why is it then that in fresh water ponds there is better productivity in warm waters?

Dr. A. Fr. **Bruun** (Denmark)—In the case of invertebrates there is a very rich production in cold waters as exemplified by cold Danish waters.

Dr. A. C. **Hardy**—As far as pond production is concerned, warm waters appear superior but not on sea fisheries.

Mr. H. S. **Swingle**—Even with regards to pond production the gauge of relative productivity should be on a uniform basis in order to avoid being misled.

Dr. N. K. **Panikkar**—We may adopt the basis on metabolism based on food.

Dr. T. I. **Storer** (U.S.A.)—On that basis it would require more energy to maintain fish in colder waters, and that may contribute to the reduced productivity in cold water ponds.

Dr. G. L. **Clarke**—But there are different species used in pondfish culture and such species are adapted to each particular condition as warm or cold water ones. So I believe the difference in productivity may not be due to the temperature as a factor but to other factors.

Paper No. 7—Seymour Sewell, R. B.—A Note on the Productivity of the Waters of the Northern Region of the Indian Ocean. (Communicated by Dr. N. K. Panikkar).

Discussion

Dr. D. J. **Rochford**—Is the silt brought down by the rivers as mentioned in this paper the same as those referred to in the previous paper of Drs. Panikkar and Jayaraman as "mud banks"?

Dr. N. K. **Panikkar**—Part of this perhaps, but not all as the mud banks are only true to certain portions of the Indian coast.

Paper No. 8—Ganapati, P.N. and V.S.R. Murthy.—Phytoplankton Production in Relation to Depth and Distance in the Bay of Bengal off the Waltair Coast. (Communicated by Dr. N. K. Panikkar).

Discussion

Dr. A. C. **Hardy**—Is the trend of abundance of the phytoplankton a continuous coordinated system or cycle that starts from the east coast to the west coast of India, or does this trend consist of independent swarms?

Dr. N. K. **Panikkar**—There is more reason to believe that the trend of abundance in different parts of the coast of India are independent of each other, although they show a consistent chronology of appearance.

Dr. D. J. ROCHFORD—Do you find a sequence of blooms by species or is there a simultaneous abundance of the species of phytoplankton encountered?

Dr. N. K. PANIKKAR—There are indications that the blooms by species follow a definite sequence.

Dr. M. JOHNSON (U.S.A.)—Can you consider the blooming sequence of the different species as an indication of some natural phenomena?

Dr. N. K. PANIKKAR—This question remains to be answered by the investigators.

Dr. J. D. F. HARDENBERG—In many instances these blooms indicate some natural phenomenon, as for instance the presence of two maxima in the plankton of a certain fish egg would show two peak periods of spawning of such species.

Dr. N. K. PANIKKAR—That is very true but it needs evidence by actual investigation.

Dr. D. J. ROCHFORD—What is the method of sampling or type of net used?

Dr. N. K. PANIKKAR—The authors did not mention it in this work.

Mr. M. A. ABAGON (Philippines)—In the Philippines we have begun investigations in the evaluation of productivity following the same line with the work of Nielsen. I believe that this is a very good index of the true productivity of an aquatic habitat.

Dr. N. K. PANIKKAR—These investigators calculated productivity on the basis of the volume. There are great variations in methods and it is really hard to claim any one method as the best one.

Paper No. 9—Cooper, L. H. N.—Some Chemical and Physical Factors Controlling the Biological Productivity of Temperate and Tropical Oceanic Waters. (Communicated by Dr. D. J. Rochford).

Discussion

Dr. R. W. HIATT—The assessment of productivity of the aquatic habitat based on the plankton by cell count is not very reliable method; so all attempts to use the techniques such as developed by Nielsen and Riley should be made.

Dr. H. S. SWINGLE—The trouble with these methods is that the procedure is too laborious. Why don't we simply base productivity on weight of fish produced? Would this not be more practical?

Mr. M. A. ABAGON—The methods put up by Nielsen and other workers in this field are much simpler, since the use of the bolting silk net is done away with. Only a pump and filter are necessary.

Paper No. 10—Hart, T. J.—The Influence of Turbulance and Vertical Exchanges on Plankton Production in the Sea. (Communicated by Dr. N. K. Panikkar).

Discussion—Reserved until all papers have been read.

Paper No. 11—Thorson, G.—The Influence of Larval Settlement upon the Composition of Marine Level Bottom Communities. (Communicated by Dr. A. Brown).

Discussion

Dr. A. W. B. Powell (New Zealand)—Similar lines of work have been undertaken in New Zealand regarding the settling of larvae at varied levels. It seems that the type of bottom is very important. It has been found that the amount of settling can now be determined by a certain formula.

General Discussion

Dr. G. L. Clarke—Three slides which form the work on the "Dynamics of Production in the Marine Area" are shown here. There are three fundamental concepts of productivity, namely: standing crop, material removed and rate of production. Another two slides show the tropic relations in the production pyramid.

Dr. A. H. Woodcock (U.S.A.)—Which of the three concepts of productivity shown by the slides do you propose as the right concept?

Dr. G. L. Clarke—All of the concepts of productivity depicted are right. It all depends upon one's viewpoint on the subject.

FISH PRODUCTION IN FRESH WATER UNITS OF JAPAN

By Katsuzo Kuronoma
Freshwater Fisheries Research Laboratory
Fisheries Agency, Tokyo, Japan

Fisheries production in the inland waters of Japan was approximately 46,000 metric tons in the year 1950, derived from the natural waters as well as through fish culture practice. This figure, though somewhat under-estimated, represents no more than 1.4 percent of the total landing of Japan's fisheries industry; but the fresh-water fish, shellfish, and shrimp are playing an important role in the nation's economy and social welfare. The present report is prepared to explain, in general terms, the productivity of fish in fresh waters of our country.

The term "production," as used in the present paper, means those fisheries products utilizable by man with economic value, and "productivity" as the capability of water to yield such products. They do not carry by any means the concept of purely biological or theoretical. The fish production by means of feeding prepared foods is not dealt with here.

The inland waters of Japan, where such production is obtainable, are diverse as to their status ranging from a small man-made pond to large lakes and rivers. The utilization of these bodies of water for fish production, or for fish propagation as called in our country, is also varied from one kind to another. Then, the writer attempted first to classify the bodies of water into five categories as listed below, considering also the means of fish production for each type.

1. *Lake:* with no artificial feeding, fish depend on natural food only.
2. *Farm-pond:* with or without artificial feeding, fish depend on prepared and natural food or on natural food only.
3. *Rice-paddy:* same as in farm-pond.
4. *Fish-pond:* always with artificial feeding, fish depend largely on prepared food.
5. *River:* same as in lake.

Such classification of inland waters by no means draws a definite line between each type, but it is believed to be sufficient to the pursuit of the present discussion.

The production of fish obtainable in any given body of water may be measured from actual yield of the animal from the water, and it is usually expressed by the total populations at a given time and also by the annual yields. The annual yields are derived from the catch statistics of either commercial basis or of sport fishing. In the case of our country, the total (yearly) populations are usually available from farm-pond and rice-paddy, but almost none of our lakes and rivers is known for its fish production as expressed by total population. The catch statistics are available on river and lake only on the commercial basis. In this country, and probably in many other countries, the figures in commercial fish catch will be far from accurate. So the productivity born in these two types of water must be understood to show only in general terms.

On the pages to follow the fish production was discussed on four types of water—lake, farm-pond, rice-paddy and river—which are exemplified by seven natural lakes, one impounded lake, four farm-ponds and three rivers, accompanied by some physiographical data in each case. For the fish yield in rice paddy, the available data are so insufficient at the present time that the explanation was limited to the mere presentation of a few examples of figures.

THE SOURCE OF DATA

The derivation of the data referred to in the present study is summarized and listed as follows in order to avoid repeated citation in the text:

1. Physical and hydrographical data:
   Tokyo Astronomical Observatory (1953), Tanaka (1913), Fisheries Agency (1952), Shiraishi and others (1953), Motoda (1950), Shiga Pref. Fish. Exp. Sta. (1952), Hokkaido Fish Hatchery (1952), Original (data in Table IV).
2. Data on catch or crop statistics:
   Statistic Section, Min. Agr. Forest. (1953); all the catch figure for 1952. Communications from Fisheries Cooperative Associations concerned; River Ishikari (1948–49), River Shinano (1948–52), River Kuma (1948–51), Lakes Kasumi and Kita (1949). Matsui (1947); all figures in Table V. Nakai and Matsui (1938); production figures around 1930 in Table II and crop figures in Table IV.

SPECIES OF FISH AND OTHER ANIMALS

The statistics show (Fisheries Agency, 1952) that the fresh water fisheries products in Japan are represented by fish (60% in weight), shell-fish (30%), shrimp and other animals, and a total of some 50 species will be fished abundant enough to be enumerated in statistics. The species listed in Table I cover all the forms of animals dealt with in the present report, and they will also fairly well represent more economically important species produced in the country. In the list are given the common Japanese name and the scientific name followed by the family to which the respective form is referred. The English names were not added in the list in order to avoid the unnecessary confusions which have been often experienced. Instead, a numerical number was given to each species in the list and the number was always suffixed to the names of animals listed in the text, which were consistently described by Japanese word.

Fish Production in Lakes

In the majority of our lakes commercial fishing of some kind or other is operated, and the total area of such lakes is estimated at 238,000 ha. by the Fisheries Agency (1952). Among a number of this particular body of water, Lake Biwa is the largest with a surface area of 67,480 ha.; and Lake Kita produces the largest amount of fish catch, 1,698,851 kgs. annually, and has perhaps the highest productivity (426.3 kg/ha.) in the country.

The fish productivity of the lakes is far better understood than that of rivers and other types of water in Japan, probably because of the easiness by which limnological as well as biological investigations have been carried out. In their study of 58 lakes of Japan, Nakai and Matsui (1938) found that lakes producing 20 to 50 kg./ha. showed the highest frequency (25.9%) in the years of the 1930's. The authors related the productivity of the lakes to their physical characters such as depth, locality, transparency, altitude, water temperature, etc. Yoshimura (1938) also discussed the relation of fish productivity of some lakes to the depth of water.

The lakes numbering eight presented here are believed to represent fairly well the physiographical as well as the biological features of Japanese lakes (Table II). It is mentioned that the seven lakes among these are of natural type, but Lake Sagami is an example of reservoir of storage type, impounded in 1945, where the fish are cropped only through the sport fishing of rod-and-line.

The fish productivity of these eight lakes are extremely varied with one another, the annual yield ranging from 3.0 kg./ha. of Lake Chuzenji to 426.3 kg./ha. seen in Lake Kita. These figures, however, show the recent trend of fish production around the year 1950, and if they are compared to the same in the years of 1930 there are found a surprising decrease of production (to 1/8 to 1/3) in the recent years except in Lake Akan, which will be touched upon later.

Within the limited given data on physical and biological character the factors effective to the fish productivity of lakes will be interpreted as follows. The physiographical factors which do not seem to be related to the productivity are the area of water, the configuration of water indicated by shore development, the altitude of the lake above sea-level and the temperature of water. Whereas, the depth of water, transparency, and productivity classes of lake (eutrophic, oligotrophic and the intermediate) will be responsible for the fish yield capability of lakes. It will be also noted that more species of fish are obtained in the high productive lakes than in waters with poor productivity (Tables II and III). All these interpretations are made possible only among the lakes enumerated here, and it is highly probable that an entirely reversed result might be reached when more examples are tested, such as was reached by Rounsefell (1946), who found that fish productivity of lakes is negatively correlated to the size of water in North America.

In Lake Kita, where probably the highest fish productivity is observed in the country, the Shijimi (24) clam holds one half of the total annual catch, followed by the small ami (21) shrimp; while in Lake Kasumi which locates side by side the former take, the ami (21) rank at the top of the catch, followed by the wakasagi (6). This fact is believed to be a good example of the high individualism of fish productivity possessed by each lake water. Lake Akan, located northernmost among other lakes shown here, is a single exception in productivity, which has increased about eight times as large as that of 20 years ago, as the result of successful transplantation of the osmerid wakasagi (6) fish in the years 1928 to 1930, the fish not dwelling in the lake before those years (Motoda, 1950).

The fish production in Lake Sagami, a reservoir, is much lower than expected, and the wakasagi (6) occupy more than half of the total catch. The low productivity of this man-made lake will be reflected by a number of factors, among which the low fishing intensity is believed to be highly responsible. We believe that the fish yield of this water will be raised, if the catch is made on commercial basis, though it is not possible at present to predict how much the productivity will be increased.[1]

The recent decrease of fish productivity is well indicated in the sampled lakes, but the same story is heard at almost any lake in the country when visited. The causes responsible for this are believed to be complex, and for the many factors picked up we are in the same opinion that the increased fishing intensity is the most effective cause. There are evidences to show that the physical as well as biological environment of our lakes has not changed so drastically as shown in fish production over a period of 20 years. In this connection the fish production in North American lakes studied by Rounsefell (1946) may be referred to with some interest; he shows that the annual commercial yield in the waters of 4,000 ha. ranges between 87.72 and 14.72 lb./acre. These figures took far below the yields experienced in our country, even if it is admitted that the fish productivity of water as well as man's activity in fisheries may be extremely varied between the two countries.

---

[1] In American lake fisheries the commercial catch is about 15 times as large as sport catch in the waters of 10,000 to 50,000 acres (Rounsefell, 1946).

Fish Production in Farm-pond

The farm-pond in Japan, called the tame-ike, is primarily used for the irrigation of the rice-paddy, and its size varies from 0.1 to 8 ha. each. At present the tame-ike of 68,478 ha. in total is now utilized by farmers for a double purpose—irrigation reservoir and fish culture pond (Fisheries Agency, 1952). The practical method of fish production is varied depending on locality of water and the people concerned. The species of fish produced in our farm-pond are the koi (12), funa (11), unagi (15), wakasagi (6) and ebi (20); also sogyo (13), masu (3) and others are often seen in the pond.

In dealing with these forms of fish the practical method of production is varied, even in the same region of the country, depending on the physical character of water, availability of fish fry, the way of draining, the demand of fish by people, and other factors. The general procedure, however, will be seen as follows: 1) the preparation of bottom bed after the drain of water (fall), immediately followed by flooding, 2) stocking of fish fry into the pond, the fry obtained usually from another body of water, and the liberation is made either in the same fall or in spring of the following year, 3) the cropping of fish during or after the drain of water (fall), the fish stocked in water for 7 to 12 months, 4) the fertilization of pond water before flooding or at proper time. It may be added that the ebi (20) shrimp are not required to be stocked every year, because some part of the population in the water are always left over after the cropping.

The productivity of fish in farm-pond, as understood from the practical method outlined now, will be affected by multiple factors, and the yields will be shown in broad range. A survey made in Kagawa Prefecture tells that the average annual crop was estimated at 151 kg./ha. in 37 ponds checked, the highest productivity recorded as 2,058 kg./ha. (Kawajiri, 1951).[2]

---

[2] The production, reaching 5,500 kg./ha. when the feeding was practiced, was seen in this survey.

A part of the original study on 4 farm-ponds, shown in Table IV, will explain the actual production of fish. Leaving the detailed analysis of data in the future, the result of study arrived at will be summarized here. The productivity, varied with each other, is correlated negatively to the volume of water held by the pond, when the volume is estimated from area and depth of pond, and the bottom vegetation, which is believed to be controlled by the character of the bottom soil and the fertility of water, has positive relation to the fish productivity. In the Onna pond a chemical fertilizer was applied, and its highest productivity is thought to be due to the effect of fertilizer. The fish yield in other three ponds, where no fertilizers were given, seems higher than that of ordinary farm-ponds in our country. It may be added that the same productivity in American farm-pond is 175 lb./acre with no fertilizer and the maximum yield of 400 lbs./acre if the water is fertilized.[3]

The species of fish in water also seem to correlate with the productivity of the pond, and we have believed in the study that: the koi (12) and funa (11), both cyprinid fish, are competing with each other in production, and the ranges of food requirement of these two species highly overlap; the wakasagi (6), a plankton feeder, is possibly and better produced in the pond with deeper water and poorer bottom vegetation; the production of the ebi (20) shrimp is limited to an extent which is determined by the population of bottom-feeding fish dwelling in the same water; the sogyo (13) does not show, in its productivity, the relation to other species.

FISH PRODUCTION IN RICE-PADDY

The fish culture practice in rice-paddy is more commonly seen than in farm-pond in Japan, but the restriction of several sorts permits such practice much less than the expectation. According to fisheries Agency (1952) the rice-paddies now utilized for fish culture measure 75,631 ha. in total area, which amounts to less than 1% of our all rice-paddies existing now. In our experience the more significant factors to determine the rice-paddy fish culture are enumerated as the soil character, availability of proper amount of water, the supply of fish fry and the traditional familiarity to fish held by farmers concerned and, needless to say, the local demand.

The species of fish raised in this particular body of water are the koi (12), funa (11) and dojo (14), also very rarely the ayu (5). Among these species of fish the koi ranked on the top of production (perhaps over 90%).

---

[3] These figures, showing the average in that country, were taken from Anonymous (1953) and Secretary of Interior (1945).

The practical methods of fish culture in the paddy field, as in the case of farm-pond, vary depending on the custom locally developed in various parts of the country. But the generalized procedure will be seen in steps as follows: 1) the preparation of the bottom bed followed by flooding of water to the depth of 10 to 15 cm. (May to June); 2) planting of rice plant shoots and stocking of fish fry (3,000 to 15,000 for each ha.), the fry obtained from another body of water or from one lot of paddy field; 3) the weeding of obnoxious grass (July to August); 4) cropping of fish which are collected in deep pools dug in front of outlets, as water level subsiding by draw down (September to October); 5) harvest of rice plant (October and November).

The productivity of fish in rice-paddy is determined again by multifold factors, which are much less understood than in the case of the farm-pond. But some of our experiments show the more responsible factors being involved in the fertilizer applied, temperature of water (usually 30°C in mid-summer), population density of fish, construction of field, amount of water, especially of its stability, strain of rice plant, natural enemy, and finally the use of herbicides, which has been becoming very popular recently.

The productivity of fish in rice-paddy is hardly mentioned at present even in general terms and the result of a small experiment, picked out from the scattered sources, is presented (Table V), which shows how fish are obtained together with rice in our paddy field. The statement expressed by Hiyama (1949) is then quoted as pertinent to this subject. He says, "The average crop of one-year-old carp (koi) when no extra food is supplied is about 130 pounds per acre."

Fish Production in Rivers

Our countless rivers and streams all produce some kind of fish which are caught by either fishermen or sport anglers, and the rivers where some sort of fisheries management is practiced are said to amount to 206,171 ha. in total area (Fisheries Agency, 1952).

The productivity of fish in rivers is hardly understood in Japan and probably in many other countries, and scientific data to show the fact are scarce and fragmentary in our country. There are several reasons which are thought to be responsible for the difficulty of obtaining data. Some of these may be briefed here. The fluctuation of water level, which is seen seasonally, is a common phenomenon in our river. The fluctuation is also made by the occasional but unavoidable visit of heavy rain storm (usually in summer and early fall) which causes the big flood over the river basin mostly very steep in Japan, with the result of nearly a complete disappearance of fish population. Also the construction of the dam, varied in size and use, is highly responsible for the fact that almost every appreciable river in the country, being turned to an un-natural flow of water, has lost its original productivity.

These facts alone have made the productivity of fish very unstable in rivers, despite the enormous effort of fish propagation practice being made. The natural as well as artificial fluctuation of water level also made it hardly possible to measure the productivity of fish in terms of kg./ha. as used in other bodies of water.

The data of fish production for three selected rivers (Table VI) of Japan are presented. These rivers, the Ishikari, Shinano and Kuma flow in the north, middle and south of the country, respectively, and it is mentioned that since each of these rivers consists of its main flow and many tributaries attached to the former, the catch statistics were so collected as to represent those mostly derived along the main flow.

It is firstly noted that River Kuma, located in the southern part of the country, shows the highest fish production considering the annual fish catch and the size of river, and River Ishikari, in northern island of the country, has the lowest production, whereas River Shinano, running in the middle part of Honshu or mainland of Japan, produces an amount of fish intermediate between the produce of the two other rivers.

As to the constitution of fish species existing, the three rivers are well characterized; the salmonoid fish represented by the sake (2) and masu (3) occupy nearly one half of the catch in River Ishikari, and in River Kuma the ayu (5) followed by unagi (9) replace, in amount, the salmonoid fish which are entirely lacking, while River Shinano is highly represented by the ugui (9) and dojo (4). All these facts will explain that each river shows its well characterized productivity and fish fauna, which are perhaps basically determined by the geographical position as well as physical environment of the river.

One of our typical rivers, River Shinano, in terms of its physiography, is then studied in order to see how fish productivity is to vary from one section to another in one system of river flow. This river, located nearly in the center of Honshu, starts in the central high mountain and runs northeast, finally pouring into the Sea of Japan. With the availability of required catch statistics the river was divided into eight sections from its estuary to the upper-reaches where the commercial fishing terminates, and the result of the study will be outlined.[4]

The fish productivity in the river does change from one section to another as expected, but it will be noteworthy to see the highest production being found, not in the lower part of the river, but in the middle of the river system (Table VII), then it graduates both up and down the river. The distribution of fish species, which has a significant bearing on the productivity, is fairly well illustrated in this river along the course of flow, and it may be concluded that each fish form has its own center or restriction of occurrence and production. The narrow or restricted distribution is shown by the sake (2), masu (3), bora (16), zarigani (23), dojo (14) and tanishi (25), all of which are produced only in the lower part of the river. The ayu (5), namazu (7), oikawa (10), koi (12) and ugui (9) are the groups of fishes which are found in the river with the center of occurrence in some part of the river, which of course varies specifically. The funa (11) and unagi (15) are evenly distributed thoroughly in the course of the river, apparently with no restriction.

---

[4] The effect of natural environment as well as fishing pressure was analyzed in each of these sections, and it will be dealt with in future.

Attempts have been made to classify, on the basis of fish distribution, the rivers and streams or to divide the single river system into regions (Van Deusen, 1953, Allee and Schmidt, 1951, and others). These authors are conservative, of course, in the presentation of their concepts, and a glance at our fish production in rivers reveals that such attempts will succeed only after a critical study of long term, but the knowledge thus obtained will become a valuable basis in the analysis of fish productivity in river and stream.

BIBLIOGRAPHY

ALLEE, W. C. and SCHMIDT, K. P. 1951. Ecological animal geography. John Wiley & Sons, New York; I-XIII, 1-713, Figs. 1-142.

Anonymous. 1953. Difference in purpose and utilization in pond fish culture. *Prog. Fish. Cult.*, 15: 38.

Fisheries Agency. Inland water fisheries and aquiculture of Japan. Fisheries Agency, Tokyo: 1-56, figs.

HIYAMA, Y. 1949. Rice-paddy carp culture in Japan. U.N. Economic & Social Council, 7/Sec/W. 70 (manuscript).

Hokkaido, Fish Hatchery. 1952. Productivity in lakes of Hokkaido (in Japanese). Material 16: 1-79.

KAWAJIRI, M. 1951. Farm-pond fish culture in villages (in Japanese). Shinshu Nogyo, Spring issue: 1-3.

MATSUI, Y. 1947. Rice-paddy fish culture (in Japanese). Tomi Shobo, Osaka: 1-166, Figs. 1-26.

MOTODA, S. 1950. Lakes in Hokkaido (in Japanese). *Hokkaido Fish Hatchery Rep.*, 5(1): 1-96, Figs. 1-66.

NAKAI, N. and MATSUI, I. 1938. Studies on the productivity of inland waters of Japan. 1. The productivity of lakes with special reference to fishery interest (in Japanese). *Jap. Jour. Lim.*, 8(3,4): 489-499, Fig. 1.

ROUNSEFELL, G. A. 1946. Fish production in lakes as guide for estimating production in proposed reservoirs. *Copeia*, 1: 29-40, Figs. 1-3.

Secretary of Interior (Letter of). 1945. Fishery resources of the United States. *79th U.S. Cong. Doc.*, 51: i-iv, 1-135, figs.

Shiga Pref. Fish. Exp. Sta. 1952. Cross-line survey of Lake Biwa for 1951 (in Japanese). *Rep. Shiga Fish. Exp. Sta.*, 3 (1) : 1-38, figs.

SHIRAISHI, Y. and others. 1953. Limnological survey of Lake Sagami, a reservoir (in Japanese, with English summary). *Bull. Freshwater Fish. Res. Lab.*, 2(1) : 31-54, Figs. 1-11.

Statistics section, Min. Agr. Forest. 1953. Fisheries statistics (in Japanese). *Agr. Fish. Statist. Mon. Rep.* 17: 65-129.

TANAKE, A. 1913. Study of Lake Suwa (in Japanese). Iwanami, Tokyo: 1-936, Figs. 1-267.

Tokyo Astronomical Observatory. 1953. Science Yearbook (Section Geography) (in Japanese). Maruzen, Tokyo: 1-186.

VAN DEUREN, R. D. 1953. A simplified technique for classifying streams useful in fishery and related resources management. *Prog. Fish. Cult.*, 15: 14-19, figs.

WELCH, P. S. 1951. Limnology (II ed.). McGraw-Hill, New York: i-xi, 1-538, Figs. 1-48.

YOSHIMURA, S. 1938. Relation between depth of lakes and the fish catch (in Japanese). *Tansui*, 1(1): 2-7, 1 fig.

TABLE I

LIST OF REPRESENTATIVE FISH SPECIES AND OTHER ANIMALS PRODUCED IN INLAND WATERS OF JAPAN, WITH THE AMOUNT OF PRODUCTION EXPRESSED BY PERCENTAGE OF TOTAL WEIGHT OF THE CATCH OF EACH SPECIES BY RIVERS AND LAKES

COMMON JAPANESE NAME	SCIENTIFIC NAME	FAMILY	PRODUCTION PERCENTAGE BY WEIGHT[1]	
			RIVERS	LAKES
Frog:				
1. Shokuyo kderu	*Rana catesbiana*			
Fish:				
2. Sake	*Oncorhynchus keta*	Salmonidae	8.4	
3. Masu	” spp.	”	1.6	1.2
4. Shirauo	*Salangicthys* spp.	Salangidae	0.9	3.8
5. Ayu	*Plecoglossus altivelis*	Plecoglossidae	13.6	3.1
6. Wakasagi	*Hypomesus olidus*	Osmeridae		11.2
7. Namazu	*Parasilurus asotus*	Siluridae		
8. Honmoroko	*Gnathopogon* spp.	Cyprinidae		
9. Ugui	*Tribolodon hakonensis*	”	4.5	0.3
10. Oikawa	*Zacco platypus*	”	2.5	
11. Funa	*Carassius auratus*	”	4.5	11.6
12. Koi	*Cyprinus carpio*	”	3.6	1.9
13. Sogyo	*Ctenopharyngodon idellus*	”		
14. Dojo	*Misgurnus anguillicaudatus* and *Cobitis* spp.	Cobitidae	0.7	1.7
15. Unagi	*Anguilla japonica*	Angullidae	4.3	
16. Bora	*Mugil cephalus*	Mugilidae		
17. Raigyo	*Ophicephalus argus*	Ophicephalidae		
18. Kajika	*Cottus pollus*	Cottidae	0.7	2.6
19. Haze	*Chaenogobius* spp. and *Acanthogobius* spp.	Gobiidae		
Crustaceans:				
20. Ebi	*Penaeopsis* spp. and others	Penaeidae		4.6
21. Ami	*Neomysis japonica*	Mysidae		
22. Kani	*Eriochir japonica*	Graupususidae		
23. Zarigani	*Cambaroides* spp.	Cambaroidae		
Molluscs:				
24. Shijimi	*Corbicula* spp.	Corbiculidae	41.2	28.9
25. Tanishi	*Viviparus* spp.	Vivaridae		
26. Tankai	*Hyriopsis, Cristaria* and *Anodonta*	Anodontidae	1.2	7.8

---

[1] Calculated from the catch in 1952 of 32 longer rivers and 37 larger lakes in the country.

TABLE II

PHYSIOGRAPHICAL CHARACTERS OF EIGHT JAPANESE LAKES WITH ANNUAL COMMERCIAL FISH CATCH

NAME OF LAKES	BIWA	KASUMI	TOWADA	KITA	SUWA	AKAN	CHUZENJI	SAGAMI [1]
Area in ha.	67,480	18,917	5,958	3,985	1,445	1,293	1,129	258
Shore development	2.61	2.62	1.64	3.78	2.61	1.86	2.02	4.76
Maximum depth in M.	96.0	7.6	378.0	10.0	7.0	36.0	170.0	36.0
Altitude above sea level in M.	86	2	401	1	759	410	1,271	155–
Temperature (°C) of surface water	7.1–28.1	2.5–28.0	3.1–26.5	3.9–27.3	0–29.3	0–23.4	1.8–21.7	6.5–26.2
Transparency in M.	3–10	2.1	18	2	3	8–9	18	0.75–3.4
Productive character [2]	0	E	0	E	E	M	0	M
Annual catch in kg. (Year)	5,545,710 (1952)	4,104,577 (1949)	31,290 (1952)	1,698,851 (1949)	447,839 (1952)	169,950 (1952)	3,393 (1952)	3,416 (1951–1952)
Production in kg./ha.								
Around 1930	469.5	875.2	5.3	2,106.0	866.0	15.28	23.39	ND [3]
Around 1950	80.86	216.9	14.21	426.3	310.0	131.4	3.0	13.6 [1]

---

[1] Lake Sagami is a reservoir, where the catch figure was obtained from sport fishing.
[2] The productive character of lake is indicated by oligotrophic (O) eutrophic (E) and mesotrophic (M).
[3] No data.

TABLE III

Fish Catch in Eight Japanese Lakes by the Percentage of Total Weight of Catch of each Fish Species

Name of Lakes (Year)	Biwa (1952)	Kasumi (1949)	Towada (1952)	Kita (1949)	Suwa (1952)	Akan (1952)	Chuzenji (1952)	Sagami (1951-1952)
1. Shokuyo kaeru		3.7						
3. Masu	1.9 [2]		94.6 [3]			1.1 [3]	71.8 [2, 3]	
4. Shirauo		5.9		1.6				
5. Ayu	8.3							
6. Wakasagi		25.7		8.9	37.9	92.7		58.5
7. Honmoroko	1.5							
9. Ugui						1.1	21.4	8.3
10. Oikawa					1.4			3.1
11. Funa	5.9	5.5		3.9	18.4	2.9	5.2	29.4
12. Koi		1.7			3.1	1.6	1.6	
15. Unagi		3.5		1.6	2.1			
17. Raigyo		1.5						
19. Haze	4.5	5.8		3.4	3.1			
20. Ebi	5.3	4.6		3.2	1.5			
21. Ami		33.2		18.9				
24. Shijimi	68.6			51.1	10.3			
26. Tankai	1.2	1.6			17.2			
Other species	2.8	7.3	5.4	7.4	4.0	0.6	0	0.7
	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

[1] A reservoir impounded in 1945.

[2] The masu, *Oncorhynchus rhodorus*.

[3] The himemasu, *O. nerka* (land-locked form).

TABLE IV

ANNUAL FISH CROP IN FOUR FARM-PONDS IN NAGANO PREFECTURE, WITH PHYSIOGRAPHICAL CHARACTERS OF PONDS AND THE PERCENTAGE OF TOTAL WEIGHT OF THE CROP OF EACH FISH SPECIES

NAME OF POND YEARS	OU 1947-1951	SHIN 1947-1948	NAKANO 1950-1953	ONNA 1952-1953
Area in ha.	3.53	2.33	1.82	0.97
Average depth in M.	2.7	3.7	2.3	1.7
Highest temperature (°C) of surface water	32.5	30.0	30.0	32.8
Bottom vegetation	Moderate	Poor	Rich	Rich
Annual crop in kg.	829.5	405.9	613.2	398.9
Production in kg./ha.	234.9	174.1	336.9	411.2
SPECIES	PERCENTAGE BY WEIGHT			
6. Wakasagi	1.8	6.2		
11. Funa	65.2	25.6	45.6	65.9
12. Koi	23.1	44.3	15.8	12.0
13. Sogyo	0.9		20.7	
15. Unagi	0.8			
20. Ebi	8.2	23.9	17.9	22.1
	100.0	100.0	100.0	100.0

TABLE V

RESULT OF THE KOI (12) CULTURE IN RICE-PADDY WITH THE CROP OF RICE AND THE FERTILIZER USED; THE STOCKING OF THE FISH LASTED 60 TO 120 DAYS WITHOUT FEEDING. FIGURES ARE ALL SHOWN IN kg./ha.

FIELD NO.	FISH	RICE	FERTILIZER
1	1,125	4,700	11,890
2	750	5,130	8,060
3	562	4,980	8,810
4	161	2,850	8,025
5	131	3,280	23,287
6	252	3,130	7,350
7	132	3,420	750
8	127	3,130	12,675
9	83	3,420	1,500
10	158	3,420	1,200

TABLE VI

ANNUAL COMMERCIAL FISH CATCH IN THREE JAPANESE RIVERS, WITH THE PERCENTAGE OF TOTAL WEIGHT OF THE CATCH OF EACH SPECIES

NAME OF RIVER	ISHIKARI	SHINANO	KUMA
Length in km.	340	328	130
Location in N. Lat.	43	37	32.30
Area of drainage basin in km.^{2}	14,250	12,260	1,970
Annual catch in kg.	266,366	892,224	560,336
(Year)	(1948–1949)	(1949)	(1948–1951)
SPECIES	PERCENTAGE BY WEIGHT		
2. Sake	41.9	7.0	
3. Masu [1]	1.7	1.3	
5. Ayu		3.2	39.6
6. Wakasagi	18.8		
7. Namazu		3.4	4.8
9. Ugui	8.2	18.9	10.8
10. Oikawa		7.2	10.6
11. Funa	7.0	9.9	3.2
12. Koi	2.1	6.4	2.8
14. Dojo	5.4	16.7	
15. Unagi		1.0	17.4
16. Bora		1.3	1.4
22. Kani	9.7		6.8
23. Zarigani		3.5	
25. Tanishi		3.2	
Other species	ND [2]	17.0	2.6
	100.0	100.0	100.0

[1] The masu, *Oncorhynchus masou* (both sea-run and land-locked form).

[2] No data.

TABLE VII

ANNUAL COMMERCIAL CATCH OF RIVER SHINANO BY SECTION OF THE RIVER AND SPECIES OF FISH, WITH THE PERCENTAGE OF TOTAL WEIGHT OF THE CATCH OF EACH SPECIES IN EACH SECTION

Sections and the distance from river mouth in km.	A(0–160)	B(161–200)	C(201–216)	D(217–248)	E(249–268)	F(269–280)	G(281–296)	H(297–328)
Approximate width of the section	120	70	70	50	40	30	20	10
Approximate altitude above sea level in M.	—	380	400	620	730	790	820	1,000
Annual catch in kg.[1]	488,122	15,543	38,932	104,973	47,482	29,456	13,050	20,433
Production in kg./km.	3,051	388	2,433	3,280	2,374	2,454	816	638
SPECIES				PERCENTAGE BY WEIGHT				
2. Sake	12.8							
3. Masu	2.5[2]	3.9[3]					0.5[4]	20.4[4]
5. Ayu	3.6	0.5		1.9	14.4	8.5	12.2	0.6
7. Namazu	3.1	10.1	12.7	3.6	2.0	1.9		2.9
9. Ugui	3.2	9.1	16.4	24.5	30.7	20.4	26.9	46.4
10. Oikawa		9.1	11.3	40.8	32.0	26.9	14.7	
11. Funa	13.4	15.8	16.9	6.2	2.3	8.9	12.7	
12. Koi	3.1	9.1	19.6	15.7	5.7	12.2	11.3	2.7
14. Dojo	29.6	16.3	2.8			1.3[5]	8.2[5]	
15. Unagi	1.0	8.4	3.8	1.2	2.7	2.6	2.6	1.0
16. Bora	2.4							
18. Kajika	1.0				3.1	0.3	4.8	15.8
23. Zarigani	6.4							
25. Tanishi	5.7	5.5						
Other species	12.2	12.2	16.5	6.1	7.1	17.0	6.1	9.8
	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

---

[1] Catch in section A for 1949, those in sections B to H for the average of 5 years (1948 to 1952).

[2] The masu, *Oncorhynchus masou* (sea-run form).

[3] The masu, *O. masou* (both sea-run and land-locked form).

[4] The masu, *O. masou* (land-locked form).

[5] The dojo, *Cobitis* spp. not *Misgurnus*.

HERBIVOROUS ANIMALS AND THE FERTILITY OF TROPICAL INLAND WATERS

By R. S. A. Beauchamp
East African Fisheries Research Organization
Jinja, Uganda

The study of tropical lakes requires a somewhat different approach from that of temperate lakes. The productivity of a temperate lake is to a large extent controlled by external circumstances, the amount of light and heat received during the course of the year. A tropical lake usually receives enough light and heat to realise its full potential productivity, and the controlling factors here are the chemical and biological characteristics obtaining within the lake itself.

A distinction must be made between fertility and productivity. A temperate lake may be fertile, or potentially productive, because it contains considerable amounts of plant nutrients in solution, yet may not be highly productive for want of the light and heat necessary to convert the inorganic salts into organic matter. A tropical lake which is fertile will also be productive at least in the sense that large quantities of phytoplankton will be produced; whether it is productive in the sense that it will support a large population of commercially valuable fish depends on the kind of phytoplankton and the feeding habits and requirements of the other animals and fish occurring in it. For instance, we have observed that in certain East African lakes blue-green algae may be abundant but, though ingested by *Tilapia*, they are not digested by these fish. The digestibility or otherwise of blue-green algae appears to be affected by the proportion of sodium to calcium ions present in the water.

It is our concern to discover what internal factors determine the various degrees of fertility shown by individual tropical waters and what factors determine the expression of this fertility in terms of fish which are valuable as food for human consumption.

The observations that follow apply only to shallow lakes and ponds situated in tropical regions. In such bodies of water the growth of phytoplankton is continuous and, unless exceptional circumstances exist, the amount of phytoplankton present is related to the total quantity of nutrients in circulation, and nutrients in solution are reduced to a low value. The current rate of phytoplankton production, as distinct from the standing crop, is controlled by the *rate* at which nutrients become available. The supply of one particular nutrient will in practice constitute the controlling factor. Nutrients commonly in short supply are nitrates and phosphates, but in East Africa we have found that some waters appear to be primarily deficient in sulphates.

Waters, which do not receive significant quantities of nutrients from their inflows and which are not fertilized artificially, depend for their nutrients on those derived by the decomposition of their own bottom deposits. Thus their fertility is determined by the nature of these deposits, and their current rate of phytoplankton production is controlled by the rate at which these deposits decompose.

A bottom deposit formed mainly of vegetable detritus decomposes slowly, whereas one containing a high proportion of animal remains, including faeces, decomposes rapidly. Thus the conversion of plant material into animal material is desirable as a means of increasing the rate at which nutrients are released and so keeping the current rate of phytoplankton production at a high value.

Not only on their death but throughout their life animals are continually breaking down organic matter and releasing nutrients. One may conclude therefore that a body of water containing a high density of herbivorous or detritus feeding animals will, under tropical conditions, have a higher continuous rate of production than one containing few such animals.

All animals which eat plant material of any sort, whether phytoplankton, rooted vegetation or detritus, are assisting in the conversion of plant material into animal material; therefore all such animals, copepods, snails, insect larvae, fish and hippopotami, must be considered as agents assisting in maintaining the fertility of the water. If the numbers of these animals were to be reduced for any reason, a higher proportion of plant material would be deposited on the bottom. Much of this material would not decompose before being overlaid by fresh deposits with the result that a gradual reduction in the quantity of nutrients in circulation would occur and this would lead to a gradual reduction in the standing crop of phytoplankton.

When considering the development of any commercial fishing in natural waters, it is therefore desirable to attempt to assess the probable effect on the herbivorous animals. In cases where the principal fishery is based on the capture of predatory fish no serious deterioration of the inherent fertility of the lake need be anticipated, but in those cases where the fishery is based on the capture of herbivorous fish, e.g. *Tilapia*, special consideration should be given to the need to maintain a considerable density of these fish. Excessive exploitation may lead not only to a reduction of existing stocks of fish, but also to a reduction in the fertility of the water in which they live.

SOME CONSIDERATIONS ON ESTUARINE PRODUCTIVITY

By E. J. Ferguson Wood
Marine Biological Laboratory
Cronulla, N.S.W., Australia

In estuarine environments, it is the bottom which controls the biology, whereas, in the marine environment the water is the dominant factor. Even in the water phase of shallow estuaries and in the intertidal zone, turbulence causes particles to be carried upwards with the minute organisms adsorbed on or lying in the surface zone of the bottom. Turbulence has a greater effect on muddy than on sandy bottoms, the effect depending on particle size. There is also greater adsorption on the smaller particles and hence, greater biological activity, e.g. bacteria are far more numerous in muds than in sands.

Muds can be for convenience divided into two groups—peaty muds including the muds of mangrove swamps, and sulphide muds where both colour and consistency are controlled by ferrous sulphide. The former oxidize slowly and the latter rapidly on exposure to air, but of course the majority of estuarine muds are a mixture of these two types in various proportions.

Estuarine muds are teeming with microbial life, and it is the complex reactions between the microbes and their chemical environment which controls the mud system. The system or biocoenosis is dynamic, and chemical analyses made at random or pure culture studies of the microbial elements give only a static picture which is only informative if we understand the dynamic processes which produce it. For example, an oxygen determination *per se* tells us nothing of the relation between photosynthesis and respiration which changes continuously with light intensity, turbidity, katabolic activity of microorganisms, consumption of plants by higher organisms, etc. Nor does the fact that *Azotobacter*, a nitrogen-fixing bacterium, is present tell us much unless it can be shown that this organism is numerically important and is actively fixing nitrogen. The chemical processes of the environment are controlled by the oxidation-reduction potential and the hydrogen ion concentration, represented by pH values. These processes may be biological or abiological, but these two divisions are not always easy to determine since microbes frequently make use of chemical transformations which release energy, e.g. the aerobic oxidation of sulphide to sulphur can occur as a chemical reaction (Verhoop reaction) or can be utilized by the sulphur bacteria to supply energy for carbohydrate synthesis. Such reactions are of course exothermic. On the other hand, organisms can carry out endothermic reactions at low temperatures obtaining the energy from an exothermic reaction. The pH values in estuarine muds usually range only between 7.5 and 8.5, while not far below the surface of a mud, the oxidation-reduction potential falls rapidly until, in extreme cases, the hydrogen line is reached. In this region, the main actors are the sulphate reducers, *Desulfovibrio, Microspira* or *Sporovibrio* as they are variously known, and a number of heterotrophic facultative anaerobes which live on the organic material produced by the autotrophs and brought in by diffusion, vertical tidal movement, etc. In some instances at least, these heterotrophs appear to produce hydrogenase which is lacking in some strains of *Microspira*. On these feed nematodes, and certain ciliates which will grow and multiply in inorganic cultures of *Microspira*.

As the redox potential increases towards the surface, the purple sulphur bacteria, diatoms (*Navicula*) and blue-green algae (*Lyngbya*) appear, the last mentioned being able to photosynthesize at Eh—50 mv. As the redox increases still more, the diatom and blue-green flora increase and become more diverse, and so do heterotrophic bacteria, iron bacteria and aerobic sulphur bacteria. In this zone, iron and sulphur are oxidized to ferric hydroxide and sulphates respectively although this oxidizing layer is not very thick.

It appears that each group of organisms has a range of pH and redox values through which it can metabolize. In some cases, these ranges overlap and we get a most complex picture of a dynamic equilibrium. It is surely not a coincidence that the region in which there is the greatest overlap is that of the seawater-mud system. Professor Baas Becking is now engaged at the Marine Biological Laboratory, Cronulla, in a study of this milieu and its chemical and physical significance, his work being of the utmost importance in the understanding of this problem.

In the formation of a new mud bank, the poised reduced milieu may reach the surface with the release therefrom of free hydrogen sulphide. More frequently however, the banks become covered with a growth of sea-grass such as Zostera, Posidonia, Ruppia or Halophila which are frequently encrusted with epiphytes and which also entrap a great deal of floating plant and animal material. This ultimately settles and is rapidly decomposed by heterotrophic bacteria which produce a strongly reducing milieu, sufficiently low in redox potential to allow the growth of *Microspira*.

Zostera and Posidonia possess in their leaves strong reducing substances which can reduce lead and cadmium salts to the metals, and which no doubt play a part in creating a reducing atmosphere in their own milieu. These plants are able to grow with their roots in muds containing free hydrogen sulphide, the root hairs being in actual contact with particles of ferrous sulphide. No explanation of this can be given.

The principal elements which are required for the adequate growth of photosynthetic plants, i.e. algae and sea grasses, are carbon, hydrogen, oxygen, sulphur, nitrogen and phosphorus. Hydrogen and oxygen are, of course, ubiquitous. The former is usually obtained from a reduced substance by enzyme or chemical activity, and I think we may say that in the muds dehydrogenation is more frequent than oxidation. Carbon is derived from carbon dioxide, which makes excess base a useful measure of the characteristics of an estuarine environment. Sulphur in its oxidized form is dissolved in seawater but is rapidly reduced to sulphide in mud. However, the sulphide is subject to rapid oxidation, both chemical and biological at the surface. Because of the activity of sulphur bacteria in the mud, sulphur dominates the environment since the reactions concerned range through about 600 mv. of oxidation-reduction potential and from about pH 9 to negative pH values, though the extreme acidity does not occur in the macro- or meso- environment. What happens in the micro-environment is a matter for conjecture.

Nitrogen is one of the controlling factors in estuarine productivity, and more work has been done on the nitrogen cycle than on any other element in the sea, notably by Waksman and his coworkers at Woods Hole. As far as estuaries are concerned we have no nitrogen balance sheet, nor do we know how to make sure of sufficient nitrogen to fulfill the requirements of the bacteria and the algae. Nitrogen is fixed in the sea by *Azotobacter*, purple sulphur bacteria and certain strains of blue-green algae, and possibly by a proportion of *Microspira* strains, but we have no estimate of the actual importance of nitrogen fixation, or of the balance between nitrification and denitrification in this environment.

Phosphorus is gradually deposited in the muds as calcium and ferric phosphates. Marine heterotrophic bacteria attack these compounds, the former very readily, the latter less readily but in significant amounts. It is not certain whether ferric phosphate is dissolved by the lowering of pH in the micro-environment during carbohydrate fermentation, or by direct utilization of the minimal amount available and continued replacement. It is known however that marine bacteria can assimilate ferric phosphate at pH 8.5.

When we consider the limitations of our knowledge, it is obvious that the random fertilization of estuaries and lagoons to produce fish is likely to prove costly and wasteful, so that a thorough fundamental knowledge of the processes involved is essential to economic husbandry.

From the economic angle, we know by observation that mullet, milkfish and other species graze on blue-green algae, diatoms and other algal forms in shallow waters; we have reason to believe that oysters, mussels, cockles and other edible shellfish digest bacteria, flagellates and other forms belonging to this environment, and that the escapement which is devoured by invertebrates can be and frequently is used by carnivorous fish such as bream, etc.

In this paper, I have merely given an outline of some of the processes in estuarine environments and a suggestion of their significance. Methodology and information on even the simplest portions of these environments is woefully incomplete, but it is now possible to detect a pattern, to determine the most important systems and to study them using simple cases, gradually synthesizing more complex combinations. Our method has been to start with inorganic components, neglecting the organic ones for the time being, adding them one at a time as we find necessary.

It will be a long time before the productivity of estuarine environments will be fully understood, and, though *ad hoc* measurements of productivity may be made by existing techniques adapted for the purpose, such measurements will not allow us to predict until we understand the dynamic forces of the problem.

SUMMARY

This paper is a consideration of some aspects of estuarine productivity from a purely qualititative point of view. Existing methodology is barely sufficient for a complete qualitative survey and totally inadequate for a quantitative one at the present moment. Fundamental studies of estuarine phenomena are essential to economic development of estuarine fisheries and to fish culture.

SOME ASPECTS OF PRODUCTIVITY IN RELATION TO FISHERIES OF INDIAN NERITIC WATERS

By N. K. Panikkar and R. Jayaraman
Central Marine Fisheries Research Station
Mandapam, India

Introduction

It is generally accepted that tropical seas are less productive than the temperate waters to the north and south of the Equator. Large concentrations of nutrients are characteristic of Polar waters and areas influenced by these waters are rich in animal and plant life. In temperate waters the nutrients accumulated during the winter months support the burst of phytoplanktonic growth which reaches its peak with increasing sunlight; the tropical waters which do not accumulate nutrients in the same manner are held not to show major peaks but an even trend of production of life throughout the year. Recent studies have, however, indicated that this concept can only be accepted with many reservations because there are known areas of high productivity in the tropical zone, where special physical factors may operate which bring the nutrient laden bottom waters to the surface. Some of these exceptionally fertile areas have been known to biologists for a long time, and fully confirmed in recent years by the phenomenal progress in Tropical Tuna Fisheries. Further, it has been indicated by many workers (Clarke, Riley and others) that the estimates made on the basis of standing crop alone cannot be taken to establish any fundamental difference in the rate of organic turnover when it is remembered that organic production takes place throughout the year in the substantially larger euphotic zone of the warmer seas.

Problems of Productivity

In comparing the organic productivity of waters of different regions, a knowledge of the distribution and seasonal cycle of nutrient salts is quite essential. There is sufficient volume of data in this respect for the waters of the temperate and colder regions. In the tropical waters, on the other hand, not much systematic work has been done and hence not much comparable data are available.

A knowledge of the distribution of nutrient salts in any area is by itself insufficient for a proper assessment of organic production.

The concentration of nutrient salts in a water mass at any time is only a momentary balance between their consumption by the phytoplankton and their regeneration by the animals. "In comparing two different water masses, a smaller average standing crop and a lower concentration of nutrient salts does not necessarily mean a smaller production of organic matter, if other conditions such as light and temperature allow more rapid growth of the plants . . ." (Harvey, 1945). The amount of nutrients in the productive zone is no doubt a measure of potential production; but the actual fertility is determined more by the rate of replenishment of nutrients at this zone than by the actual concentration observed at a particular time (Ketchum, 1947). The replenishment is provided by decomposition and water circulation. When there is active regeneration *in situ* in the surface layers, the nutrients are readily available for organic production. If the regeneration takes place in the deeper waters, as is more often the case, the regenerated nutrients have to await transport to the surface layers before being made available for consumption by plants.

It may therefore be seen that the assessment of organic production in an environment does not lend itself to direct attack; several of the factors enumerated above have to be considered before arriving at any estimate of production. A knowledge of the distribution of nutrients is, however, considered to be the basis on which various theories of productivity have been founded.

Its Application in the Indo-Pacific

The subject is of interest and importance because of the search for more food from the seas in areas situated within the tropical belt where the population pressure is high, rendering the development of additional sources of food from the sea a world necessity. Many countries within the tropical zone and especially those bordering the Indian and Pacific Oceans are taking active interest in the development of their fisheries. A discussion on this subject is therefore most appropriate because apart from the value of such a discussion in assessing the present views on the problem, it would help focus attention on aspects of research requiring close attention in these countries. Any lead which these discussions could give to develop and orient the research programmes would be of practical benefit in the mobilization of scientific effort in an area which is admittedly backward in both equipment and personnel.

There is ample evidence to show that even within the tropical zone as elsewhere, there are areas which are both highly productive and comparatively barren. In many instances the reasons for such marked differences within closely adjoining areas and in the same latitude are not fully understood. An intergrated oceanographical and fisheries programme might perhaps give us some explanation. In areas where fish landings could be studied and different regions compared some idea of comparative productive value of adjoining waters could be gathered. What is equally necessary is the research on productivity which could precede exploitation to map areas which may have potentially valuable fisheries at present unutilized.

Sea Fisheries of India

It is clear from a study of the sea fisheries of India that very marked differences exist in the amount of fish production on the two coast lines of India lying in about the same latitude. Table I shows the production of sea fish from the various sectors of the Indian coast line as estimated by statistical samplings of fish landings by indigenous crafts. With the exception of a small number of powered vessels operating from Bombay and which at present do not substantially affect the total yield of sea fish, the fish landed in India come entirely from the landings of indigenous craft and gear working only within the narrow strip of the coast line mostly within five miles and in any case not exceeding ten miles from the shore. The fish are therefore entirely from neritic waters, although not all areas lying within the continental shelf are fished.

TABLE I

Production of Sea Fish in India

Zones	Extent of Coastline in Miles	Average Annual Catch for 1950-52 (In Tons—2,224 lbs.)	Annual Catch per Mile
East Coast:			
1. West Bengal & Orissa	369	8,825	23.92
2. Andhra coast (south of Gopalpur to north of Visakhapatnam)	159	31,561	198.50
3. Andhra coast (Visakhapatnam to Masulipatnam)	194	30,878	159.16
4. Andhra coast (south of Masulipatnam to north of Pulicat Lake)	249	954	3.83
5. Coromandel coast (Pulicat Lake to Cuddalore)	139	17,518	126.03
6. Coromandel coast (south of Cuddalore to Devipatnam)	222	8,299	37.38
7. Palk Bay & Gulf of Manaar	240	8,144	33.93
West Coast:			
8. Travancore, Cochin and South Malabar (Cape Comorin to Ponnani R.)	263	117,010	444.91

9. Malabar & South Kanara (north of Ponnani R. to Mangalore)	171	118,136	690.85
10. Kanara, Karwar & Konkan coast (north of Mangalore to south of Ratnagiri)	307	64,144	208.94
11. Bombay & Gujarat coast (Ratnagiri to Broach)	386	113,666	294.47
12. Kathiawar coast (Broach to Pakistan Border)	500	16,582	30.48
All-India Total	3199	535,716	165.19

The figures bring out clearly that of the total sea fish production of the country, between 65 and 75 per cent comes from the west coast of India and only the remainder is caught on the east coast. The west coast fishermen are no doubt better organized and able to take advantage of the harvest, but the difference in production is not entirely due to this because there is a corresponding reduction in the per capita landings between the east and west coasts. Even the best fished areas of the east coast do not compare favourably with any strip of the west coast of India. If a closer analysis is made of the different zones of the west coast, it becomes clear that the higher landings are to the south, the highest landings being on the Malabar Coast with the Travancore-Cochin coast coming next.

What are the features that go to make the west coast of India so highly productive as compared with the east coast in the same latitude? Hydrologically, the Bay of Bengal and the Arabian Sea seem to present substantially different features although the differences in temperature and salinity are not appreciable. A fairly clear picture of the hydrology of the two seas is available from the work of Sewell on the 'Investigator' and the results of the John Murray Expedition on the Arabian Sea.

Hydrological Background

Although information on the water masses forming the Indian Ocean is by no means complete, the general ideas have been summarized by Schott (1935) and Sverdrup *et al.* (1943). The waters include three distinct components, viz. the Indian Equatorial water, the Indian Central Water and, running between the depths of the above two, the Deep waters of the Indian Ocean which is continuous with the Antarctic bottom waters. The latter drift into the Indian Ocean in a few distinct regions, a tongue of it proceeding in the direction east of Madagascar and grazing the Seychelles/Mauritius bank, the second moving in the direction of the Carlesberg submarine ridge and a third forming an arc converging on the southern part of India and Ceylon in a southeasterly direction, but later going round Ceylon, one branch going westward in the direction of the Laccadive-Maldive Archipelagoes and the other entering the Bay of Bengal. High salinity waters from the Red Sea enter the western part of the Arabian Sea and generally the salinity of the Arabian Sea is higher than that of the Bay of Bengal, the latter also being substantially influenced by the large volumes of fresh water brought down by the numerous rivers. It may be generally said that the waters of the Arabian Sea, being part of the Indian Ocean, are of an oceanic character while that of the Bay of Bengal are predominantly of the estuarine type. The temperatures in both the seas generally range from 25° to 30°C, with values between 21° and 25°C during the monsoon months in some areas near the coast. Annual amplitude is normally within 2°–5°C. in the Bay of Bengal and 3°–5°C. in the Arabian Sea. Areas of higher amplitude are seen at the head of the Bay of Bengal (5°–10°C.) and the Gulf of Oman.

It has been indicated from the results of the John Murray Expedition that the influence of the bottom Antarctic waters which come to the surface when these waters strike the submarine ridges in the Mascarene bank and the Carlesberg-Murray ridges is most marked in increasing the productivity of the surface waters. The areas which are particularly rich are to the east of Seychelles-Mauritius Bank. The general oceanic concept that deep moving waters come to the surface when confronted with submarine ridges is generally employed in the explanation of the richer areas in the Arabian Sea.

The Arabian Sea and the Bay of Bengal are subject to the monsoons. The strong southwest monsoon winds on the east coast of Africa driving waters away from the shore results in the upwelling of waters which forms a northerly current, the Somali current which flows along the east coast of Africa, later towards northeast in the direction of Arabia, finally moving south along the coast line of India. Sewell has pointed out that the cause of the rich fisheries in the west coast of India is to be sought in this current which brings in its train the cold waters rich in nutrients. It seems probable that the rich coastal fisheries off the Arabian, Mekran and Pakistan coasts are formed as a result of this current, but it is for further investigation as to how far the current grazes further south and influences the fisheries.

Special Features of the West Coast of India

The bulk of the west coast fisheries in the highly productive zones of Travancore-Cochin and Malabar is constituted of plankton feeding fishes, the Sardines and Mackerel, which account for about 30% and

25% respectively of the total catches. The former group includes several clupeoids of the Genus *Sardinella* and related forms, but the most valuable is the oil sardine of Malabar, *Sardinella longiceps.* The mackerel is composed only of one species, viz. *Rastrelliger kanagurta.* Both the fisheries extend from almost the southernmost part of the peninsula to some distance south of the Bombay coast. There is a distinct and unmistakable gap in the distribution of the major fisheries to the north of Ratnagiri. North of this place shoals of mackerel are not known, but the species is certainly widely distributed having been found in the Persian Gulf and in the Bay of Bengal and stray specimens have also been taken in the trawls operated off Kathiawar. Smaller shoals of mackerel have been encountered near the coast in the Bay of Bengal at several places. Although both the species are widely distributed in the Indo-Pacific, the special reason why large shoals occur only in the Travancore-Cochin, Malabar and the Konkan coasts is a problem which requires examination. If, as is assumed, the nutrient laden current supporting the rich plankton extends from the northerly direction, the fish should occur in shoals at much higher latitudes and further the shoals appear first in large numbers towards the equator and then only spread to the north. Purely on distributional grounds it would be reasonable to expect the shoals getting their sustenance from the southeast part of the Arabian Sea, and at least as far as the mackerel and sardine fisheries are concerned, it is probable that either the coastal turbulence following the southwest monsoon or local upwelling between or near the Laccadive-Maldive Archipelagoes are probably significant.

Mud Banks of the Malabar Coast

The Malabar coast has also certain characteristic physical features which would appear to play an important role in the retention and release of nutrients to the coastal water. Soon after the monsoons, fine particles of silt become distributed in the coastal waters and with the decline in strength of the winds and currents, this silt settles in the form of fine mud forming a bank extending from about the region of Alleppey to the areas north of Calicut. The mud bank is fluid and movable and exists often at sub-surface levels in the form of fine silt in the process of settling and geologists believe that its occurrence and movements are somewhat connected with the heavy monsoon rainfall of the Malabar coast, the weight of the large amount of water that is brought down into the coastal tracts pressing out the soft mud from its subterranean formation. Whatever be the explanations for the formation of the mud bank, the fact remains, as has been conclusively demonstrated by my colleague Seshappa (1953), that large quantities of nutrients, especially phosphates, are found in the interstitial waters of these mud particles. Apart from dissolved phosphates there is also a large quantity of adsorbed phosphates which is released into the waters when the mud bank is agitated. The highest phosphate values are during the monsoon months June–July with subsequent smaller increases in the North-East monsoon of the September–November period. The exact relationship of the mud bank formation with the Fisheries yet remains to be elucidated, but it is an aspect of marine studies which seems to require development in tropical areas subjected to strong currents and winds. Its relationship to plankton production is also important because the banks render the waters turbid substantially reducing the depth of the euphotic zone.

Swarming of Planktonic Species

Enrichment of surface waters by upwelling or other physical agencies is also illustrated by the widespread prevalence of planktonic outbursts of small flagellates, the dinoflagellate, *Noctiluca,* and the blue green alga *Trichodesmium.* On the Malabar coast the swarming of *Noctiluca* is known to cause abrupt setbacks in Fisheries (Bhimachar and George, 1950) and such instances are not unknown on the east coast of India (Madras, Aiyer, 1936). Swarming of flagellates on the Malabar coast has been known to cause mortality of fishes. These flagellates have been termed differently by various authors, but it has recently been shown by Subrahmanyan (1953, unpublished) that it is a member of the Chloromonadinae, belonging to a genus new to science. In the Palk Bay area a sudden increase in numbers of *Noctiluca* is known to reduce the output of the sardine fisheries (Prasad, 1953) and unpublished observations of Prasad and Jayaraman (1953) indicate that swarming of *Noctiluca* also introduces noteworthy chemical features like increase in the amount of silicates, and it may be recalled that abnormal increases in the amount of phosphates have been recorded by Ketchum and Keen (1948) following the red tide in the Florida sea water.

The general effects of animal exclusion caused by dinoflagellates have been discussed by Sproston (1949) and other authors. From the results available it is also fairly clear that the periods of diatom intensity in the plankton vary very much in the various sectors of the Indian coast. The results at Waltair are given by Ganapati and Murthy (1953, this Symposium). In Madras further south of Waltair, the diatom peak is in May with a secondary maximum from November to January, and the lean season for diatoms is from July to September (Menon, K. S. 1931). At Mandapam in the Gulf of Manaar the principal peak period of diatoms is in May and there are other periods of maxima in February–March and again in August–November; the lean period is from December to January (Prasad, 1953 unpublished). At Trivandrum, the peak period is in May, but the lean period is in December (Menon, M.A.S. 1945). In Calicut on the other hand the peak period is in May, but there again secondary maxima are observed in January–February and again July–August (George, P. C. 1953). Investigations carried out in successive years have shown that there are quite often shifts in the periods of intensity and the occurrence of several minor peaks not usually observed in the colder waters. Further it is worthy of note that while a general peak can only be made out from the total number of various species, there are varying individual peaks for several species even in months other than in the collective peak periods. This has been specially brought out by detailed work on diatoms carried out at West Hill by Subrahmanyan (Unpublished). These results would indicate that the problems of diatom production and the subsequent effects of grazing by the zoo-plankton are much more complex in warmer waters where the phytoplankton and zoo-plankton maxima are not produced by any one or two species but by a large variety of species having varying periods of maxima and minima. It has to be ascertained to what extent the individual maxima of the various species are caused by physico-chemical factors or whether they are purely caused by biological sequences and also whether large scale planktonic outbursts of flagellates, *Noctiluca* and *Trichodesmium,* could be taken as indicative of abnormal turbulence, raising nutrients available in surface waters far above normal.

Seasonal Cycle of Nutrient Salts

Systematic studies on the distribution and seasonal cycle of nutrient salts in the Indian coastal waters have been undertaken in recent years at the Central Marine Fisheries Research Station, Mandapam, South India. The data reported in this note were collected between 1948 and 1953 at selected inshore stations in the Arabian Sea (West Coast–off Calicut) and in the Bay of Bengal (East Coast–off Madras city and off Mandapam). The following tables give the average monthly concentrations of the nutrient salts–phosphates and nitrates–in the inshore waters on both the west and east coasts. The annual ranges for phosphates and nitrates in the English Channel have also been included in the tables to serve as a basis for comparison.

TABLE II

Average Monthly Values for Phosphates in Four Places in S. India (Neritic Waters)
Phosphates Expressed as ug—at P/L.

	Off Madras City 1948-49	(Bay of Bengal) Off Mandapam * 1950-53	Off Mandapam ** 1951-53	(Arabian Sea) Off Calicut 1948-53	English Channel
January	0.50	0.20	0.20	0.48	Winter
February	0.40	0.22	0.21	0.40	maximum in
March	0.36	0.24	0.18	0.40	different
April	0.40	0.18	0.18	0.41	years:
May	0.45	0.18	0.17	0.70	0.47—0.70
June	1.00	0.26	0.25	0.89	
July	0.90	0.23	0.17	1.06	Summer
August	1.05	0.23	0.17	0.84	minimum in
September . . .	0.70	0.22	0.21	0.85	different
October	0.48	0.18	0.21	0.72	years:
November	0.35	0.20	0.23	0.64	0.02—0.10
December	0.30	0.15	0.18	0.53	(Harvey, 1945)

---

* Gulf of Manaar.
** Palk Bay.

TABLE III

Average Monthly Values for Nitrates—
Nitrates Expressed as ug.—at N/L.

	Off Madras City 1948-49	(Bay of Bengal) Off Mandapam ** 1950-53	Off Mandapam * 1951-53	(Arabian Sea) Off Calicut 1951-53	English Channel
January	2.0	2.9	4.0	5.6	Winter
February	1.1	3.2	3.2	8.3	maximum in
March	3.2	3.1	3.5	4.8	different
April	2.0	3.2	3.3	3.4	years:
May	Data not	2.4	2.9	16.3	6.0—7.0
June	available	2.0	3.7	10.6	
July	8.6	2.5	3.2	15.5	Summer
August	4.6	2.6	3.3	10.6	minimum in
September	2.8	2.1	3.8	2.4	different
October	3.0	2.7	3.4	3.5	years:
November	2.6	3.0	3.8	0.5	0.0
December	1.8	2.9	4.4	2.8	(Harvey, 1945).

---

* Gulf of Manaar.
** Palk Bay.

It will be seen from these tables that there are considerable variations in the distribution of nutrient salts in the waters of the two coasts and also in different areas on the same coast. In the waters of the Arabian Sea and in the Bay of Bengal off Madras city the phosphates are found to occur in very high concentrations. Distinct seasonal cycles of phosphates have been observed in the inshore waters of the Arabian Sea. In this area, the phosphate values are very high during the period of the Southwest monsoon, May to September. The nitrates are also high during the same period. It may thus be noted that during the Southwest monsoon, the surface waters off the west coast are replenished with nutrient salts to a considerable extent. The rate of replenishment also seems to be quite high. It is therefore, possible that the productivity, which depends a great deal on the rate of replenishment, is also high.

A comparison of the values of nutrient salts in the waters of the Arabian Sea with the range of concentrations reported for the waters of the English Channel shows that the total turnover of nutrient salts in the former area is somewhat higher than in the latter. If conditions such as temperature, light intensity, etc. are favourable, as is usually the case in the tropical waters, the total production of organic matter per unit area would appear to be higher in the waters of the Arabian Sea than in the English Channel. Although much more data are necessary, it seems safe to conclude that the production is at least of about the same order as is observed in most temperate waters.

The distribution of nutrients in the waters of the Bay of Bengal off Mandapam presents an entirely different picture. The level of nutrients in these waters is in general much lower than in the other areas. Seasonal variations in the concentrations of nutrients are also very small. Of the two areas studied near Mandapam there are differences in the amount of nutrients available at Palk Bay and in the Gulf of Manaar, the former generally showing slightly higher values. Studies on plankton show that likewise, Palk Bay appears to show a higher plankton production as compared with the Gulf of Manaar (Prasad, Unpublished). These require much closer study in relation to succession of organisms. The work so far carried out has only shown how difficult it is to form generalized conclusions even within adjacent areas.

CONCLUSION

The evidence brought forward and the views expressed at this symposium have certainly indicated the need for more intensive work on marine problems in any effort to open up new areas for fishing. An energetic and integrated programme on Oceanography and Fisheries in tropical waters may well result in much information of value to dispel the belief prevalent among many that tropical sea fisheries cannot be developed because there are no fish in those waters, and which may pave the way for developing new food resources in the Indo-Pacific area.

ACKNOWLEDGMENT

We are indebted to many of our Colleagues of the Central Marine Fisheries Research Station and its substations whose data, collected individually and collectively, have in parts been reported in this paper and discussed.

REFERENCES

AIYAR, R. G. 1936: Mortality of Fish of the Madras Coast in June 1935. *Curr. Sci.* IV, No. 7.

BHIMACHAR, B. S. and GEORGE, P. C. 1950: Abrupt Setbacks in the Fisheries of the Malabar and Kanara Coasts and 'Red Water' Phenomenon as their Probable Cause. *Proc. Ind. Acad. Sci.* XXXI, No. 6.

CLARKE, G. L. 1946: Dynamics of Production in a Marine Area. *Ecol. Monogr.* 16, 321-35.

GANAPATI, P. N. and MURTHY, V. S. R. 1953: Phytoplankton Production in Relation to Depth and Distance in the Bay of Bengal off the Waltair Coast. *Proc. Eighth Pac. Sci. Cong.* III-A, 1145-1155.

HARVEY, H. W. 1945: Recent Advances in the Chemistry and Biology of Sea Water. Cambridge Univ. Press: 1-164.

KETCHUM, B. H. 1947: Biochemical Relations between Marine Organisms and Their Environment. *Ecol. Monogr.* 17: 309-315.

KETCHUM, B. H. and KEEN, JEAN. 1948: Unusual Phosphorus Concentrations in the Florida 'Red Tide' Sea Water. *Jour. Mar. Res.* 7: 17-21.

PRASAD, R. R. 1953: Swarming of Noctiluca in the Palk Bay and Its Effect on the 'Choodai' Fishery with a Note on the Possible Use of Noctiluca as an Indicator Species. *Proc. Ind. Acad. Sci.* XXXVIII, Sec. B. No. 1, pp. 40-47.

————. 1953: The Marine Plankton Characteristics at an Inshore Station in the Gulf of Manaar near Mandapam (Unpublished).

PRASAD, R. R. and JAYARAMAN, R. 1953: Preliminary Studies on Certain Changes in the Plankton and Hydrological Conditions Associated with the Swarming of Noctiluca (Unpublished).

SCHOTT, G. 1935: Geographie und Oceanographie des Indischen und Stillen Ozeans. Hamburg.

SESHAPPA, G. 1953: Phosphate Content of Mud Banks along the Malabar Coast. *Nature*, London, 171, 526-27.

SEWELL, R. B. S. 1937: Oceans round India. From "An Outline of the Field Sciences of India." Ind. Sci. Congr. Assn. 18-41.

SPROSTON, N. G. 1949: A Preliminary Survey of the Plankton of the Chu-San Region with a Review of the Relevant Literature. *Sinensis*, 20: 58-161.

SUBRAHMANYAN, R. 1953: On the Life History and Ecology of *Hornellia marina* Gen. et. sp. Nov. (Chloromonadineae), causing green discoloration of the sea and mortality among marine organisms off the Malabar coast (Unpublished).

SVERDRUP, H. U., JOHNSON, M. W. and FLEMING, R. 1942: The Oceans, Their Physics, Chemistry and Biology. Prentice Hall, New York.

FACTORS FOR FISH PRODUCTIVITY

By A. G. Huntsman
Fisheries Research Board of Canada
St. Andrews, N. B., Canada

Certain facts gave the generalizations that in the northern hemisphere there are more kinds of animals toward the equator and that there are more individuals toward the pole. The latter at least is to be seriously questioned. At the poles there is little of the sunlight that is necessary for life and the temperature is unfavorably low. At the equator there is much sunlight and the temperature, at least in the water, is not unfavorably high.

What then are the facts responsible for the idea prevalent for the northern hemisphere that northern waters are rich and southern waters are poor, and how are the facts to be explained? Off the eastern coast of Canada two currents come together, one from the south, the Gulf Stream, which brings warm water with few organisms of very many kinds, and the other from the north, the Labrador Current, which brings cold water with many organisms of few kinds. This occurs near 45° north latitude, that is, in the middle of the temperate zone. But organisms live longer at low temperatures than at high temperatures, and long life permits a large stock to accumulate where productivity is low. Productivity cannot be safely judged from the numbers of individuals present at one time, the standing crop. The best evidence of productivity is the quantity of organisms that can be removed steadily over a long period, e.g. pounds of fish taken regularly each year.

Facts for production in enclosed ponds under control negate the idea that there are more individuals produced each year towards the poles. The highest regular production of fish, of which we know, has been obtained near the equator. In Madras, India, the Dykes tank with an area of 2½ acres produced 10,798 pounds of fish (mainly of the genera *Catla, Cirrhina, Labeo* and *Thynnichthys*) in four years from 1946 to 1949, which is an average of more than a thousand pounds per acre per year (Anon. 1952b). In Java, brackish ponds have an average production of as much as 380 pounds per acre of milkfish (Chanos) and have at the same time produced as much as 830 pounds of prawns (Penaeids) which would mean as much as a thousand pounds per acre per year (Schuster 1952). There are higher figures, but these seem to be with addition of food. Embody (fide Viosca 1937) gives an upper limit of 600 lbs. per acre for latitudes from 37° to 40° in the United States; and in Germany with a latitude near 50°, carp ponds produce up to 348 lbs. per acre (Viosca 1937), although with the use of sewage the yield "would seem to be over 1,000 pounds per acre." To have higher production in the tropic zone is in accord with light and temperature suitable for growth being greatest in amount for the year near the equator. It would appear that under favorable local conditions productivity is highest in the tropic zone.

Data on the quantities of fish removed annually from the different waters in commercial fisheries are far from being satisfactory for comparisons in productivity. Such as they are, however, they do give provisional indications of comparative productivity. It can always be claimed that the catches of fish do not represent what might be taken and that they are unrepresentative of actual productivity in the various regions. Nevertheless, they have certain significance, which we should try to judge. A recently published map (Anon. 1952a) attempts to show the world distribution of the catches of fish and the figures do reveal greater catches in the sea in the temperate zone than in the tropic in the northern hemisphere on both sides of both Pacific and Atlantic oceans, but a great decrease to the Arctic and on the whole a decrease from the tropic zone through the south temperate zone to the Antarctic. Let us first consider the general difference this means between the northern and southern hemisphere. The most recent figures obtained and published by FAO (Gerhardsen 1953) shows only about 6½% of the world catch of fish to be reported from the southern hemisphere. This seems anomalous since more of the water is in the southern hemisphere and more of the land in the northern hemisphere. The contrast is even greater if the earth is divided obliquely to place the greatest amount of water in one hemisphere, which then has only about 3½% of the total catch. This might be interpreted as the result of the people that catch and use the fish being on the land, which is undoubtedly an important factor. However, it is true that in a region with great fisheries, such as the North Atlantic in the temperate zone, the fish caught not only are taken but are produced close to the shore and that, where the water is very deep, not only is there no commercial fishing, but also fish are undoubtedly scarce per unit of area. In very deep water far from land, there is relatively little life of any kind, and there is generally a decrease in the organic content of the bottom sediments going from shallow to deep water (Sverdrup *et al.*, 1942). Moreover, the amounts of phosphate and nitrate which are essential for plant growth, are quite low in general over great depths in the superficial water where alone there is sufficient light. These facts seem to signify that high production is a coastal phenomenon, that is, it occurs in shallow water along the coasts of continents, whatever factors are involved.

The most recent data available for the landings of fish on various parts of the west coast of the North Atlantic Ocean (Table I) show highest production in the temperate zone and particularly between latitudes 35° and 45°. However, the very high production is related to the densest human population on land and the fish landed are not all caught off the same part of the coast. Also, considerable quantities of fish taken off the northern parts are landed in Europe. The International Commission for the North Atlantic Fisheries is now trying to determine the catches of groundfish made each year in each one of clearly defined statistical areas along the northern part of the west coast of the Atlantic, and the best figures yet available are those for 1951. They show (Table II) highest production between 43° and 52°. Baffin Island is included in place of Greenland because it is on a more direct course to the pole. It is probable that the catch per 100 miles of ocean frontage was almost as high for the Newfoundland areas as for the Maritimes. From these facts it would seem that production of fish along ocean coasts is highest in the temperate zone and drops off gradually to low levels in the tropic zone. Toward the north pole it drops off quite abruptly to amounts that are practically negligible. It should be noted that the somewhat similar picture on the eastern coast of the North Atlantic Ocean shows, in correspondence with temperature and with a greater total catch of fish, the highest production considerably farther north. For example, on the east Barents Sea north of the Arctic Circle is quite productive, while on the west Hudson Bay south of the Arctic Circle has practically no fishery. It is quite clear that little sunlight and low temperature greatly reduce fish productivity in the arctic polar zone. It does seem also that productivity on ocean coasts is low in the tropic zone as compared with the temperate zone. The fishermen of Spain and particularly Portugal, with tropic waters comparatively near at hand on the coast of Africa, cross the North Atlantic Ocean to obtain fish on the Newfoundland banks in the temperate zone. This fact definitely negates any idea that African tropic coastal waters are rich in fish, which are not taken because no proper fishing effort has been made.

What factors are responsible for the high productivity in certain localities in the temperate zone? This question had been studied in the Maritimes area and a provisional answer is now advanced. So many factors come into play that it would be unwise to state why any locality either in the tropic zone or in the temperate zone has a low or high productivity until the local conditions have been investigated. Differences in productivity can be provisionally attributed to the differences in local conditions with which they are found to be consistently correlated.

The increased productivity of the Labrador Current as it brings water from the Arctic, where there is too little light and too low a temperature for much plant growth, to northern Newfoundland is doubtless owing to increase in light and to rise in temperature with passage into the temperate zone. With light temperature suitable for growth, productivity is found to be limited by availability of the necessary materials or organisms, starting with nutrient salts for the plants and ending with fish for the fishermen. At every stage in the chain of production, what is taken must be in sufficient concentration where and when the taker operates. Otherwise production slows up or stops altogether. In a pond the taker and the taken are close together and production proceeds space. Nutrient salts, such as phosphates and nitrates, are firmly held by plants and finely divided soil, as witness the growth of plants on the side of a hill which is frequently drenched with rain. In the sea they are similarly held by animals and bottom silt and for the most part at much deeper levels than the well-lighted surface layer to which plant growth is confined. Although the sea water circulates, the rate at which deep water rich in nutrient salts comes near the surface varies greatly from place to place. This process seems to be the important one for plant productivity in the sea rather than any contribution of these salts to the sea in river discharge. The comparative barrenness of deep water is evidently owing to slow replacement from the depths of the nutrient salts used in plant growth near the surface. Waters in the temperate region that become rich at the surface during the winter when plant growth ceases rapidly, become poor with the spring growth of the plants. Renewal comes with the turnover in winter cooling of the surface water. The richness of the water of the North Atlantic drift as it passes northward along the coast of Europe may be the result of continual overturn with passage into progressively cooler regions. The marked changes in temperature during the year in the temperate zone are very effective in bringing deep water to the surface. Even the daily changes in temperature effect some overturn, though to no great depth, and ensure more vertical circulation of water. Winds may mix the water to a considerable depth, particularly where large waves break along a coast and over banks. It is possibly significant that the great fisheries are in regions characterized by progressive cyclonic storms. Tidal currents through narrow channels and over shoals are very potent in bringing deep water to the surface and in mixing it with the superficial water, because they act regularly about every six hours. Discharge of fresh water from rivers is of considerable importance, not in contributing nutrient salts but in making the deep water light when mixed with it and thus ensuring that it remains near the surface. The local productivity of plants in warm seas depends in general upon the rate of replacement in the surface water of the nutrient salts in short supply during the favorable season for growth. Knowledge of such replacement is needed. The heavy tidal action in the Bay of Fundy brings rich bottom water and even bottom particles to the surface. The particles make the water more or less turbid and thus cut down the light that is available in the water for growth of plants. Consequently, the relatively light water that issues from the Bay into the Gulf of Maine is rich for continuous growth of plants as it moves near the surface along the coast of Maine (Gran and Braarud 1935). Strong tidal action in the St. Lawrence estuary at the inner end of the deep Laurential Channel brings deep water to the surface and mixes it with the fresh water of the river (Huntsman 1923). The relatively light and rich water thus produced spreads out at the surface of the southern part of the Gulf of St. Lawrence and is evidently responsible for the exceptionally rich fisheries of that region (Huntsman 1932).

Unless the fish are sufficiently concentrated in the particular place and at the particular time, fishing is unprofitable. In water 100 fathoms deep, even a thousand pounds of fish per acre would mean for 10-pound fish that no two would be as close to each other as 60 feet when uniformly distributed, which would make their capture very difficult. Concentration of the fish near the bottom or near the surface is fairly general and is a distinct aid to their capture. Fish that keep to a certain depth below the surface and wander, tend to be concentrated near the bottom along the contour line for their depth, which means that they are along the coast. For example, fish that are during most of the day at a depth of five fathoms will be mainly found along the contour line for five fathoms. The circulation of the water has been found to determine the concentrations of herring and salmon in the Bay of Fundy. Herring in their late larval stage are concentrated from the Gulf of Maine and Bay of Fundy into Passamaquoddy Bay (Huntsman 1952a). There, at a later stage, they are captured in fixed shore traps, called weirs, as concentrated locally by wind currents and by the circulation set up by discharge of river water and by its mixture with the heavier salt water through tidal action (Huntsman 1934). The salmon of the Saint John River are distributed in the sea along the river outflow for about fifty miles, and whenever they cease feeding and wander near the surface, they become concentrated toward the river mouth by the deeper current that offsets the outflow of salt water. This concentration ends at the reversing falls in Saint John harbour where that current ends when it provides salt water for mixture with the fresh in the reversing falls. Where thus concentrated, 70% of the local salmon are taken in drift nets, but half-way out along the outflow only 20% are taken, and near the outer end so few that fishing is unprofitable (Huntsman 1952b). A somewhat similar circulation of the water, but horizontal rather than vertical (Huntsman 1952b), concentrates salmon of the inner Bay of Fundy at the outer end of Minas Channel against the Nova Scotian shore, where they are taken in weirs.

Fish, such as herring and salmon, are dependent for growth upon having animals suitable for their food quite near at hand, a matter of inches rather than of feet. Wandering may bring them near their food, but on the whole they are carried by currents when not near the bottom and may thus be concentrated where food is plentiful or scarce. Herring reflect in their fatness the local availability of food (Battle *et al.,* 1936) and high production results from concentration of the young herring and suitable food together in Passamaquoddy Bay (Huntsman 1952a). The food of larger herring as it happens, consists of large copepods and euphausiids which are most abundant in somewhat deep water where there are no herring. Salmon have been found to grow particularly rapidly in Cobsquid Bay, where the local production of food is very low through marked turbidity of the water, but where suspension of silt by strong tidal action buoys them and food animals up together near the surface, thus making feeding easy.

It is evident that the copepods and other animals, which feed upon minute plants such as diatoms, depend for growth upon the local availability of the later. Copepods that are carried into Minas Channel and the inner part of the Bay of Fundy, whether from without or from within, are found to be in poor condition and moribund (E. Jermolajew in Huntsman 1952b). Conditions there in turbidity and vertical movement are such as to keep the numbers of plants at a very low level.

To sum up: Except when water is quite shallow, production of fish is high only when there is a combination of favourable conditions. There must be sufficient sunlight. The light must not be stopped by turbidity from penetrating deeply into the water. The temperature must be sufficiently high. The nutrient salts for plant growth must be steadily brought near the surface (where alone there is sufficient light) from the bottom where they tend to accumulate and be held. The minute, floating plants must be where the small animals are that make use of them. The small animals must be concentrated together with the fish that feed upon them. The fish must be concentrated so that their capture is sufficiently easy. High fish production tends to be a decidedly local matter. The tropic zone has most favorable light and temperature, but lacks the changes in temperature and the frequent storms that renew surface fertility in the temperate zone.

TABLE I

FISH PRODUCTION (LANDINGS) IN 1949 ON VARIOUS PARTS OF THE WEST COAST OF THE ATLANTIC OCEAN FROM THE NORTH POLE TO THE EQUATOR IN RELATION TO LATITUDE AND OCEAN FRONTAGE. DATA FROM GERHARDSEN (1953), ANDERSON AND PETERSON (1952) AND MARSHALL (1952).

PART OF COAST	OCEAN FRONTAGE (English miles)	RANGE IN LATITUDE (°)	LANDINGS OF FISH (millions of pounds)	LANDINGS PER 100 MILES (millions of pounds)
Greenland	1,100	60-73	55	5
Newfoundland, Labrador and Quebec	1,400	47-61	742	53
Maritime Provinces of Canada	400	43-47	581	145
New England	400	41-45	1000	250
Middle Atlantic States	200	38-41	521	260
Chesapeake	150	36½-38½	335	223
South Atlantic States	900	25-36½	405 (1945)	45
West Indies	1,400	12-24	64	5
Venezuela and Guianas	1,500	5-12	185	12

TABLE II

GROUND FISH PRODUCTION (CATCH) IN 1951 IN VARIOUS STATISTICAL AREAS OF THE NORTH WESTERN ATLANTIC OCEAN AS REPORTED BY THE INTERNATIONAL COMMISSION FOR THE NORTHWEST ATLANTIC FISHERIES (COTE 1952). IN ADDITION, 534 MILLIONS OF POUNDS CAUGHT ARE NOT DEFINITELY REFERABLE TO PARTICULAR AREAS, BUT ARE MAINLY REFERABLE TO THE NEWFOUNDLAND AREA.

AREA	OCEAN FRONTAGE (English miles)	RANGE IN LATITUDE (°)	CATCH OF FISH (millions of pounds)	CATCH PER 100 MILES (millions of pounds)
Baffin Island	1,100	61-74	0	0
Labrador	700	52-61	65 +	9 +
Newfoundland	700	47-52	748 +	107 +
Maritimes	400	43-47	614	154
New England	350	40-44	441	126

REFERENCES

ANDERSON, A. W. and C. E. PETERSON. (1952). Fishery statistics of the United States, 1949. *U. S. Fish and Wildlife Serv., Stat. Dig., 25*, pp. 1-298.

ANONYMOUS. (1952a). *FAO Fisher. Bull.*, 5, (3-4), p. 136.

————. (1952b). Hydrobiology of department waters. *Progr. Rep. Madras Rur. Piscicult. Scheme*, (1950-1951), Sect. C., Pt. VIII, pp. 35-41.

BATTLE, H. I., A. G. HUNTSMAN, A. M. JEFFERS, G. W. JEFFERS, W. H. JOHNSON and N. A. MCNAIRN. (1936). Fatness, digestion and food of Passamaquoddy young herring. *J. Biol. Bd. Can., 2*, (4), pp. 401-429.

COTE, J. (1952). Statistics of landings of groundfish from the convention area. *Am. Rep. Inter. Comm. N. W. Atl. Fisher., 2*, pp. 35-68.

GEHARDSEN, G. M. (Ed.). (1953). 1950-51 Yearbook of fisheries statistics. Food. Agric. Organ. Un. Nat., pp. 1-296.

GRAN, H. H. and T. BRAARUD. (1935). A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine including observations on hydrography, chemistry and turbidity. *J. Biol. Bd. Can., 1*, pp. 279-467.

HUNTSMAN, A. G. (1923). The influence of tidal oscillations on vertical circulation in estuaries. *Trans. Roy. Soc. Can.*, Ser. III, *17*, Sect. V, pp. 11-14.

————. (1932). Relation of biology to oceanography. *Bull. Nat. Res. Council* (U.S.), *85*, pp. 520-536.

————. (1934). Herring and water movements. Univ. Liverpool, James Johnstone Memorial Volume, pp. 81-96.

————. (1952a). How Passamaquoddy produces sardines. *Fundy Fisherman, 24*, (24), p. 5.

————. (1952b). The production of life in the Bay of Fundy. *Trans. Roy. Soc. Can.*, Ser. III, *46*, Sect. V, pp. 15-38.

MARSHALL, H. (1952). Fisheries statistics of Canada 1949 and 1950. Canada Dept. Trade Com., Dom. Bur. Stat. pp. 1-96.

SCHUSTER, W. H. (1952). Fish-culture in brackish-water ponds of Java. *Indo-Pac. Fisher. Connc., Spec. Public., 1*, pp. 1-143.

SVERDRUP, H. U., M. W. JOHNSON and R. H. FLEMING (1942). The oceans. New York, pp. 1-1086.

VIOSCA, P. (1937). Pondfish culture. New Orleans, U.S.A. pp. 1-260.

THE PRODUCTIVITY OF TEMPERATE AND TROPICAL WATERS

By R. S. Wimpenny
Fisheries Laboratory
Lowestoft, England

The fishery production of tropical, temperate and polar seas is alike dependent on the production of plankton and primarily the unicellular algae of that community. These in turn are limited by the availability of substances such as nitrates and phosphates, which may be in short supply and are often found to be completely exhausted in the upper illuminated zone. However, in the Antarctic the supplies of these nutrients have been found to be so great that even after the maximum growth of a copious algal plankton they were not completely consumed at the surface.

Our picture of the supply of nutrients is that there is always a large amount in the deeper waters of the sea beneath the photic zone. This supply is brought to the surface in the winter in polar and temperate seas by more or less extensive vertical mixing (turbulence) but the degree of this varies and in the middle of the summer it is liable to be reduced to a quite shallow layer caused by the warming up of surface water. This means that when the algae have used up all the nutrients in the layer, no more may be expected and growth ceases until the layer breaks down in the autumn. This type of shallow surface water isolation caused by temperature discontinuity is especially characteristic of temperate seas.

Some investigators in this field (7) have put forward the thesis that there is an optimal depth and speed for vertical turbulence. If this works down through too short a range all the nutrients are used up and isolated from further supplies. On the other hand, if it goes too far down below the illuminated region, the algae are carried down below the range of the light too long and die, subsequently sinking. Over-active turbulence in shallow water may be harmful either by the small particles of bottom mud, sand or detritus reducing light penetration, or by these particles absorbing essential nutrients. In tropical oceans light penetration is deep and vertical mixing constant with the result that any nutrient brought into the illuminated zone is synthesized as soon as it appears and is therefore kept at a level which is either low or undetectable.

Although, on the whole, it looks as if the supply of nutrient salts to the surface algae may be better in high latitudes, it must not be forgotten that the continuous use and return of nutrients by algae could maintain the nutrients at a low level while a high rate of supply was being maintained. Finally, in weighing the availability of limiting nutrients in tropical seas against those of higher latitudes, it must be borne in mind that areas of upwelling off the west coasts of Africa and South America may maintain substantial quantities at the surface.

On this physical foundation the greater part of the plankton observations made on deep sea expeditions in the last sixty years has indicated a somewhat variable standing crop with a tendency to show higher values at high latitudes. The "Deutschland" expedition to the Atlantic in 1911 may be taken as an example. Here Lohmann (16) found that in the tropics the microplankton per litre of sea water could be counted in thousands, in temperate oceanic water in tens of thousands, and in temperate coastal waters in hundreds of thousands. The observations made by the expeditions have also been borne out of counts of diatoms made throughout the annual cycle in coastal waters at different latitudes. At Low Isles in the tropics the average daily number of diatoms counted in a litre was 5,793 [Marshall 1928–29 (17)], off Plymouth 14,282 [Lebour 1915 (15)] at La Jolla 39,994 [Allen 1922 (1)], and at Loch Striven 1,009,100 [Marshall and Orr 1926 (18)].

A collection of estimates of the standing crops of plankton worked out as equivalent dry weights has been made by my colleagues, Dr. D. H. Cushing and Mr. J. C. Corlett, but is not yet published. By their courtesy, however, I have been able to look at their figures and these, although they show some series of ascending values with latitude, are too variable in their disposition in time and place to allow of a critical judgement of this question.

Of the direct dry weight estimates of zooplankton that have been made, the work of Corlett in the Barents Sea (4) and Wimpenny in the North Sea (23) has produced results from Hensen net hauls for June in the years 1949–1952 that may be compared (32, 45, 13 and 24 against 44, 43, 43 and 97). These results were expressed as dry weight per metre cubed and in three out of the four years the North Sea value was higher. This difference, however, may be more apparent than real as the season of maximum development may be later in the Arctic than in the North Sea. Moreover, the North Sea stations were closer to the land in very much shallower water subject to more mixing and coastal run-off.

In addition to these observations on the standing crop there have been a number of indirect estimates of minimal production of organic matter—often expressed as tons of carbohydrate under a square kilometer. These have been made by obtaining the equivalent changes between maximal and minimal phosphate, other nutrients, and carbon dioxide in relation to the corresponding dry weights or wet weights of algae (10). Oxygen production has also been used over short periods in black and white bottles in order to obtain the net production due to photosynthesis (6). The results showed that there appeared to be better minimal production in the Arctic [Krebs and Verjbenskaya (14)] than in the English Channel [Atkins (2)], the relation being expressed as 348 to 612 tons of carbohydrate under a square kilometre in the former area compared with 250 tons in the latter.

While up to this point the general view was that production in the sea generally tended to increase with latitude, the work of Riley (19) has divided opinion on this matter. Working on a range of stations in the North Atlantic and measuring the production of oxygen by algae at different depths, Riley found that, if one considered the greater depth to which light penetrated in the tropics, as much or more production was going on at the tropical stations than at those further north. In spite of this, more zooplankton was found to be supported at the northern stations. It may be that the greater production at the tropical stations was capricious or seasonal.

Quite recently Steemann Nielsen (20), who has criticized Riley's methods, has experimented with the rate at which radio-active carbon is taken up by photosynthetic organisms and his first results, although admittedly incomplete, support the thesis of somewhat poorer productivity in the tropics. Riley, on the other hand, considers organic production in all seas to be much the same.

From the foregoing I think we may conclude that, as far as standing crops of plankton are concerned, we are likely to find higher values in higher latitudes, but the relative total production achieved in high and low latitudes is still somewhat of an open question with the most recent method of appraisal thought to favour the thesis of poorer tropical seas.

Ascending the various levels of production to the point where it interests us as food, I give below a series of annual values for commercial fish landings in thousands of metric tons taken from the FAO Yearbook of Fishery Statistics for 1950–51. I have picked out the more important countries and divided them into two groups, first those lying roughly north of Latitude 30°N. and second those between Latitude 30°N. and Latitude 30°S. The fish referred to are mainly marine.

North of 30°N.		
Russia	1800	
Europe	3900	
Japan	3796	
Korea (N)	1326	(1938)
Korea (S)	628	(1938)
Canada	948	
U.S.A.	1583	(1946)
	13,981	

30°N. to 30°S.		
Africa	800	
India & Pakistan	905	(1950)
Ceylon	37	
Indonesia	420	(1949)
Malaya	177	
Indo-China	410	(1949)
Australia	46	(1950)
Philippines	266	
Mexico	55	(1950)
Brazil	155	(1950)
Peru	84	(1950)
Venezuela	78	(1950)
	3,433	

Of these two groups, it is seen that the total catch is substantially lower in the tropical and sub-tropical countries. Of course, these areas have not been so extensively exploited by modern methods as some of those further north and when these have been used there have been cases where very good yields have been obtained. An instance of this sort is afforded by the catch of 281 cwts. per 100 hours fishing by a 77-ft. motor trawler using a 50-ft. headline trawl in the Gulf of Paria (20). This is a rate of fishing over twice as high as that usual for a southern North Sea motor trawler in 1951. But it must be remembered that a virgin ground was being fished and that it was a ground in receipt of the rich run-off from a tropical river. Another case is afforded by the Castle type steam trawl "Raglan Castle" (3) which, as a result of five years' work on the grounds between India and Ceylon, showed a rate of fishing of 53 cwts. per day's absence, a rate higher than that of British near water trawlers, but lower than that of those working the Iceland grounds. Finally, the figures for the small trawler fleet working out of Sidney, New South Wales, in 1938 gives a catch of 21 cwts. per day's absence and 260 cwts. per 100 hours' fishing (5). These trawlers may be directly compared with the Milford Haven hake trawlers of the same size and gear type, which were catching 118 to 120 cwts. per 100 hours fishing in 1938 (12). They were not, however, fishing as well as British Iceland trawlers which were catching 1.33 cwts. per 100 hours' fishing in that year.

Against these moderate successes are to be set some less encouraging results. In 1921 and 1922 a Castle type trawler, the "William Garrick," working off the Indian coast near Bombay was only able to land fish at the rate of a little over 103 cwts. per 100 hours' fishing (11). Again, in 1926, 1927 and 1928, another Castle type trawler, the "Tongkol" (8 & 9) worked the extensive fishable banks between Malaya, the East Indian Islands and Indo-China. Using a 110-ft. headline trawl she was not able to maintain a fishing rate of 80 cwts. per 100 hours. Both these rates are below that at which Castle type trawlers would have fished in the poorer areas around the British Isles. No sustained efforts have been made to introduce European methods of fishing other than trawling to the warmer seas, but it should be mentioned in passing that initial experiments with the Danish seine in Ceylon (3), Egypt (22), and Malaya (8), and with a powered boat using drift nets in the sea near Ceylon (3) have given unpromising results.

On the evidence to date, therefore, I conclude it likely that tropical seas are less productive of fish than those of higher latitudes, although I do not believe the disparity is so great as was formerly thought. If this is in fact so, it would perhaps be helpful to think of some reasons which operate in favour of inferior production in these areas, and I have set down below some which suggest themselves to me.

1. The supply of plankton food on which the fish ultimately depend and which is indicated by the standing crop may be generally inferior to that found further north or south.

2. High temperatures are likely to increase the respiratory rate of algae more than the photosynthetic rate and production will be reduced.

3. When the plankton food is the same or even higher, it is often more widely dispersed owing to the deeper photic zone. The greater dispersion makes food harder to get, involving the use of more energy in its pursuit and so leaving less available for the building up of body tissue and food reserves.

4. Probably as a result of the higher temperatures of the environment, the communities of commercial fishes and their food are much more complicated and are divided into a larger number of species in warmer seas. These complicated communities imply species linked together in long food chains or highly modified to obtain a special food with considerably greater effort than is necessary in the cooler waters of the world. Both these arrangements mean a wastage of potential production in the use of extra kinetic energy.

5. Owing to a higher metabolic rate, it is likely that tropical and semi-tropical fish find it more expensive in food to maintain the same unit weights as in cooler seas. When food is lacking, as the breakdown rate is likely to be greater, there will be an increased mortality.

To test the validity of these reasons it will be of first importance to carry out critical tests to determine whether or not basic organic production is or is not lower in tropical seas and this, I think, may well be done by an extension in areas and season of Dr. Steemann Nielsen's C_{14} method. On top of this it will be necessary to determine the utilization of algal production by animals at different levels, and I think, in particular, to set up tank experiments to determine the wastage of production due to its utilization by a differentiated community. Tank experiments on the efficiency of food utilization by fish at different temperatures have also an urgent claim on the time of research workers in this field where physiology and ecology adjoin each other so closely.

Finally, it must be said that while expectations from the sea may not appear so good for tropical as for non-tropical countries, there are indications that the bias in freshwater fisheries is in the other direction. Evidence that has been discussed recently by Dr. C. F. Hickling, Fisheries Adviser to the Colonial Office (13), suggests that tropical countries may look hopefully to relatively high production of freshwater fish in ponds as an important reinforcement of their animal protein resources. It appears that fish produced in fertilized fish farm ponds, particularly those of the carp varieties are capable of much superior growth in the tropics, yields of 3,500 and 4,000 lbs. an acre a year in Malaya and South China, comparing with 168 lbs. in Central Europe. One of the reasons for this difference between the state of affairs in the sea and in freshwater is almost certainly the fact that the winter temperatures fall much lower in freshwater than in the sea as one leaves the tropics, and the result is that growth is interrupted seasonally for longer and longer periods. Apart from this, however, within the tropical and semi-tropical zones there are wide differences in the yields that may be obtained from fertilised ponds and there is no doubt that systematic studies on the physiology and genetics of tropical pond fishes will produce information to explain these differences and to ensure the application of methods designed to secure the best yields.

BIBLIOGRAPHY

1. ALLEN, W. E. 1927 & 1928. *Bull. Scripps Instn. Oceangr.* Tech. Ser. I. pp. 19-29, 31-38 and 357-401.
2. ATKINS, W. R. G. 1922. *J. Mar. Biol. Ass. U.K.* XII, pp. 717-771.
3. CEYLON GOVERNMENT. Administration Report of the Acting Director of Fisheries for the Years 1940-1950 and 1951, Colombo, 1952.
4. CORLETT, J. C. 1955. *Annales Biol.*, IX, In press.
5. FAIRBRIDGE, W. S. 1948. *J. of Council for Scientific and Industrial Research, 21*, pp. 75-98, Melbourne.
6. GRAN, H. H. 1927. *Rep. Norw. Fish. Mar. Invest. 3*, pp. 1-74.
7. GRAN, H. H. and T. BRAARUD. 1927. *Journ. Biol. Board of Canada, 1*, pp. 279-427.

8. **Green**, C. F. and W. **Birthwhistle.** 1927. Reports on the S. T. "Tongkol" for the Period 25th May to 31st December 1926. Government of Singapore.
9. ————. 1928. *Ibid.* for the year 1927.
10. **Harvey**, H. W. 1950. *J. Mar. Biol. Ass. U.K.* XXIX, pp. 97-137.
11. **Hafford**, A. E. 1923. Report on the Work of the Steam Trawler "William Garrick." Government of Bombay.
12. **Hickling**, C. F. 1946. *Min. of Agric. and Fish., Fish Invest. Serv. II.* XVIII, No. 1, pp. 1-59 London.
13. ————. 1948. *Nature, 161*, pp. 748-751.
14. **Krebs**, E. and N. **Verjbenskaya.** 1932. *J. du Conseil.* VII, pp. 25-46.
15. **Lebour**, M. V. 1917. *J. Mar. Biol. Ass. U.K.*, XI, pp. 133-182.
16. **Lohmann**, H. 1920. *Arch. Biontol.* IV. Heft 3. pp. 1-617.
17. **Marshall**, S. M. 1933. Great Barrier Reef Expedit. II, No. 5, pp. 111-157.
18. **Marshall.** S. M. and A. P. **Orr.** 1927. *J. Mar. Biol. Ass. U.K.* XIV, pp. 837-868.
19. **Riley**, G. A. 1929. *J. of Mar. Research*, II, pp. 145-162.
20. **Steemann-Nielsen**, E. 1952. *J. du Conseil.* XVIII, pp. 117-140.
21. **Whiteleather**, R. T. and H. H. **Brown.** 1945. An Experimental Fishing Survey in Trinidad, Tobago and British Guinea. Anglo American Caribbean Commission, Washington.
22. **Wimpenny**, R. S. 1932. Report on the Fisheries of Egypt for the year 1930. pp. 1-113. Government Press, Cairo.
23. ————. 1953. *Annales Biologiques*, IX, In press.

A NOTE ON THE PRODUCTIVITY OF THE WATERS OF THE NORTHERN REGION OF THE INDIAN OCEAN

By R. B. Seymour Sewell
Zoological Laboratory
Cambridge, England

The basic guide to the productivity of the ocean is to be found in the amount of the nutrient salts, e.g., nitrites, nitrates, phosphates, etc., that are found in the water; and these nutrient salts are largely derived from the bacterial decomposition of decaying organic matter. This bacterial activity probably takes place at all depths and perhaps most efficiently on the sea bottom; but there is a zone in which it is marked in Indian waters at a depth of some 40–300 metres depending on the locality and the season of the year.

In the Arabian Sea and its offshoots, the Gulf of Aden and the Gulf of Oman, the peak amount of nitrate present in the upper waters is situated as follows:

Gulf of Aden	*Depth*	*Stations*	*Month*
(a) Head of Gulf	80 m.	19, 21 and 17	September
" " "	c. 200 m.	197 and 199	May
(b) Entrance of Gulf	40-100 m.	23, 30, 31, 32 and 35	October
" " " below	200 m.	174, 181, 182 and 183	May
Arabian Coast	50-80 m.	41, 43, 46, 51, 52 65, 68 and 76	October
Gulf of Oman	80-100 m.	60, 61, 69, 81, 82, 83, and 92	November-December
Arabian Sea	100-200 m.	97, 99, 100, 101, 102, 116, 117 and 118	December-January
" "	150-300 m.	127, 129, 130, 131, 132, 134 and 136	February-March
" "	200-300 m.	166, 167, 169, 171 and 173	April

By the process of photosynthesis these nutrients are utilized and are built up by the phytoplankton and other chlorophyl-bearing plants into organic substances and the amount of nitrate in the upper stratum above 60 or so m. is usually rapidly reduced in concentration. The photosynthetic zone extends downwards to the "compensation point," at which the intake of oxygen just balances the output by photosynthesis: Gilson (1937) has shown, from observations taken by the John

Murray Expedition 1933–34, that the productivity zone in the Arabian Sea sinks during the calm weather between September and February by about 55 metres and during this period the amount of nitrate present at this depth fell from 290 to 30 mg.N/m^3, which indicates "a consumption of at least 200 mg.N/m^3 in a layer of water 55 m. thick and a production of algal material of 14.4 grm/m^2/day.

Gilson (1937, p. 65) has also pointed out that at the lower limit of the photosynthetic zone there is abundant organic matter and since the growth of phytoplankton is prevented by lack of light there will also be ample nitrate available. We may therefore anticipate that "in areas where there is any considerable production of plankton, the presence of nitrate-reducing bacteria would be reflected in a high nitrite concentration at this level. As we have already seen, this is normally the case in the open sea." Rakestraw (1933) has put forward the same origin for the nitrite found about the 40-metre level in the Gulf of Main. At most stations the peak of the nitrite-concentration occurs at a level just below the zone of maximum productivity, and it is specially prominent at levels at which a rapid change of density of the sea-water, e.g., a thermocline, tends to hold up the sinking of organic particles. This level varied from 10 to 200 m. depth, but in the majority of the 'John Murray' observations between 30 and 150 m. depth:

Between	10 and 20 m.	depth	...	2	occasions.
"	30 and 40 "	"	...	8	"
"	50 and 80 "	"	...	11	"
"	100 and 150 "	"	...	9	"
At	200 m.	depth	...	1	"

It is interesting to note that it is from the 150 and 250 m. depth that the bulk of upwelling water is brought to the surface. Phenomenally high nitrite concentrations were recorded between 150 and 600 m. depth at Stas. 61, 82, 84 and 92, and at 1000 m. depth at Sta. 83, and Gilson tentatively suggests that this may perhaps be connected with the azoic character of the sea-floor in this region. Accompanying this high nitrite concentration it was found that the oxygen content was remarkably low.

It is generally stated that the phytoplankton is sparse in tropical waters; but this is true only for the open sea away from land. Riley has concluded that, although phytoplankton is sparse in tropic waters, the low concentration of the breeding stock is partly counterbalanced by the great depth of the photosynthetic zone and the concentration of nutrients is kept very low by rapid utilization rather than by lack of available supply; and Seiwell's work (1935) in the North Atlantic points in the same direction.

The sparseness, or otherwise, of the phytoplankton must depend on

(1) The rate of multiplication of the individual organisms, and in tropical seas this is probably far more rapid than in temperate or cool waters.

(2) The rate of consumption of the phytoplankton by herbivorous predators.

(3) The death-rate, from lack of oxygen, of organisms that have sunk below the 'compensation level,' and

(4) A sufficient supply of 'trace elements,' such as iron, which are necessary for profuse growth, and of other chemical substances, such as "auxine" and Trihydrone which may stimulate profuse growth.

In estuarine regions the growth of phytoplankton may be so profuse that it dominates the type of plankton, whereas in open waters in the tropical zone of Indian Seas, the plankton is usually of the zooplanktonic type. This profuse growth of phytoplankton in such coastal waters is probably due to several causes, among which the following may be recognised:—

> The influx in solution in the river water of a large supply of nutrient salts, nitrates, phosphates, etc. due to (a) the contamination of upstream or coastal areas by the insanitary habits of the local population; (b) the effect of tropical thunderstorms, that produce large quantities of nitric acid. This may amount to tons of acid per square mile (*vide* Ross and Bagchi, 1925). Such acid will combine with alkalies to form nitrates which may be swept into the rivers and any excess that is carried into the sea will react with calcium carbonate and will prevent the growth of coral and equally of their symbiotic Zooxanthellae, thus leaving such nitrate as may be present for the growth of diatoms. The presence at Sta. 134 to the west or the Maldive Archipelago of water of high nitrate concentration and low salinity, accompanied by a profuse growth of phytoplankton, is attributed tentatively by Gilson to the outflow of low salinity water following the Northeast Monsoon from the Bay of Bengal and its further transport westwards into the Arabian Sea.

Braarud and Klem (1931) have shown that in the area investigated by them, the coastal waters of Norway, the addition of nutrient salts from land was insignificant; but in tropical regions, where severe thunderstorms are of frequent occurrence, especially during the monsoons, and the habits of the local population are insanitary, the opposite may well be the case.

The plankton population in the coastal regions of the Indian and Burmese peninsulas may be remarkably rich at certain seasons of the year. Menon (1931) has recorded that there is on the Madras coast a barren period in August and September; but this is followed by a gradual increase in the amount of the phytoplankton in October–December, followed by a slight fall in January–February and then by a primary maximum in April–July. On the west coast of India there is a diatom scarcity in September reaching its lowest level in December; and thereafter in January–February there is a secondary rise, with a slight fall in March and then a primary maximum in May. He attributes these differences on the two sides of the peninsula to the different character of the monsoons on the two coasts. At times the efflorescence of diatoms may be so profuse as to cause a noticeable discolouration of the surface water. The production of 'Red Water' by the growth of the alga *Trichodesmium erythraeum* is a well known phenomenon and Alcock (1902) has recorded that on one occasion between Pulicat and Madras the sea surface as far as the eye could reach was thickly covered with a sort of floury yellow dust, composed of threads of diatoms, each thread consisting of about 100 individuals. Unfortunately he does not give the actual date of this occurrence, but, judging from the "Investigator" Station List, it must have been in March of 1889 or 1890.

Discolouration of the surface water may be due to organisms other than diatoms. I have myself seen the sea surface off the west coast of India exhibiting a marked Port-wine colour that was due to enormous numbers of Coccolithophoridae. Discolouration of the water by Dinoflagellates is of relatively frequent occurrence off the West coast of India; and within my own experience I have seen the sea covered with a green scum in Mergui estuary, S. Burma, in December, 1913, and a brick red scum off the South Arabian Coast in a region of upwelling water in October, 1933, caused by Noctilaeas.

In certain regions there may be a profuse growth of plant life, which is not planktonic, as for instance, the profuse growth of *Sargassum* weed around the islands off the South Arabian coast or around the Moscos islands, Burma, or of the cotyledonous plant *Cymodocea;* but the greatest amount of plant life is to be found in coral reefs, for these are largely composed of Lithothamnion, and in the symbiotic Zooxanthellae, which infest not only the coral polyps but also a number of other animals that live on the reefs, such as the mollusc *Tridacna.* The actual relationship of the Zooxanthellae to the coral polyp is still a matter of some doubt, but there can be no doubt that they must contribute very largely to the well-being not only of the coral polyps but also of the rich and varied fauna that lives on the reefs: Yonge (1936, 1940) concludes that the Tridacnidae consume great numbers of Zooxanthellae and so thereby obtain "significant amounts of food" and he has suggested that this association between corals and Zooxanthellae may be "an indispensable factor in the necessarily great powers of growth and repair possessed by the marine *communities* known as coral reefs."

Figures for the amount of algal production in different parts of the ocean are as follows:—

English Channel.	Atkins	(1923)	8.3	grm/m^3/day (wet weight)
" "	Cooper	(1933)	8.3	"
Clyde.	Marshall and Orr	(1927)	26.6	"
Bergen.	Gran	(1927)	6.7	"
Rondalsfjord.	Gran	(1929)	2.4-9.94	"
Lofoten.	Foyn	(1929)	18.6	"
Barents Sea.	Kribs and Verbinskaya	(1932)	29-56	"
Tropical Atlantic.	Seiwell	(1935)	12.7	"

Excluding the Barents Sea, this gives an average value of 11.66. Gilson's (1937, p. 59) estimate for the Arabian Sea is 14.4 grm/m^3/day, but he considers this to be too low for the rich area at the mouth of the Gulf of Aden and probably too high for most of the Arabian Sea: but he admits that "whatever the value of the comparison, it is probably safe to say that the productivity of the tropical upwelling areas exceeds that of any temperate sea, while the open tropical ocean is by no means as barren as has commonly been supposed and is indeed comparable in this respect with a region such as the English Channel," and he warns us that "the total population (of the phytoplankton) is not necessarily a true measure of the productivity, if we define productivity as the rate of carbon assimilation and cell increase."

Reference List

Alcock, A., 1902, A Naturalist in Indian Seas. John Murray, London.

Braarud, T. and Klem, A., 1931. Hydrographic and Chemical Investigations in Coastal Waters of Norway. *Hvalradets Skrifter*, No. 1.

Gilson, H. C., 1937, Chemical and Physical Investigations. The Nitrogen Cycle. *Sci. Rep. John Murray Expedition, 1933-34.*, II.

Menon, K. S., 1931, A Preliminary Account of the Madras Plankton. *Rec. Ind. Mus.*, XXXIII.

Rakestraw, N. W., 1933, Studies in the Biology and Chemistry of the Gulf of Maine; (1) The Chemistry of the Waters of the Gulf of Maine in August, 1932. *Biol. Bull.*, LXIV.

Ross, W. C. and Bagchi, K. N., 1925, The Seasonal Variation in the Reaction and Hardness of River Water in India. *Indian Journ. Med. Res.*, XII.

SEIWELL, H. R., 1935, The Annual Organic Production and Nutrient Phosphorus Requirement in the Tropical Western North Atlantic. *Journ. Cons. Explor. Mer.*, X.

YONGE, C. M., 1936, Mode of Life, Feeding, Digestion and Symbiosis with Zooxanthellae in the Tridacnidae. *Sci. Rep. Great Barrier Reef Exped.*, I, No. 11.

————, 1940, The Biology of Reef-building Corals. *Ibid.*, I, No. 11.

PHYTOPLANKTON PRODUCTION IN RELATION TO DEPTH AND DISTANCE IN THE BAY OF BENGAL OFF THE WALTAIR COAST

By P. N. Ganapati and V. S. R. Murthy
Andhra University
Waltair, India

Introduction

Sewell (1913) gave the earliest account of the plankton of the Bay of Bengal, based on a large number of collections made at different stations in the coastal region of southwestern Burma, south of the Gulf of Mataban, during the survey seasons 1910–1912 from R.I.M.S.S. "INVESTIGATOR." He found that while the plankton in the northerly region exhibited a regular banded arrangement divisible into four productive areas, the more southerly region showed a more uniform distribution of plankton. He also found that the quantity of plankton obtained at various stations varied considerably and that the surface plankton was more abundant towards the southern end of the area under investigation than in the more northerly region. Other plankton investigations in the Bay of Bengal have so far been largely confined to the coastal waters not extending beyond 2 to 3 miles from the shore, the collections being made from crude country crafts like the catamaran, by the fishermen. On the southwest part of the Bay of Bengal off Madras city, Menon, K. S. (1931) and Aiyar *et al.* (1936) studied the qualitative and quantitative distribution of the plankton during the various months of the year. Chacko (1950) investigated the seasonal variations of the planktonic organisms in the Gulf of Mannar for the period of 1940–43. Raghu Prasad *et al.* (1952) made a preliminary survey of the distribution of plankton at six inshore stations in the Gulf of Mannar during January to March 1951 and found that there was unevenness in the distribution in the area surveyed. In addition to these general investigations of the plankton on the east coast of India, accounts of special groups of planktonic organisms such as Actiniaria (Panikkar 1936, 1947), Zoantharia (Menon 1927), Medusae (Menon, M. G. K. 1932, 1936, Nair 1951), Polychaete larvae (Aiyar (1933), Chaetognatha (John 1933, 1937; Varadarajan & Chacko 1943), Copepods (Sewell 1912, 1929, 1932), Thaliacea (Sewell 1926; Nair 1949) Fish eggs and larvae (John 1951) are also available.

Seymour Sewell (1929) carried out a series of investigations on the surface waters of the Bay of Bengal from the southern extremity of Ceylon in longitude 80°E to Duncan passage in 93°E during the years 1914 and again from 1921 to 1925, from the R.I.M.S.S. "INVESTIGATOR." He collected water samples for salinity analyses and temperature readings were also taken down, every four hours. Combining his own data with those of the previous workers' like Dallas (1887) and Mathews (1926), Sewell prepared a series of four charts showing the isohalines in the Bay corresponding to the seasons September to November, December to February, March to May, and June to August and showed how the isohalines were influenced by the prevailing currents during the various seasons. Jayaraman (1951) surveyed the salinity conditions and distribution of nutrients in the Bay of Bengal off Madras city during 1948–49. Raghu Prasad (1952) during a cruise in August 1950 from Trincomalee to Calcutta back to Madras and then to Mandapam made observations on the temperature gradient and light penetration in the upper 200 feet layers. La Fond (1953) investigated the environmental factors affecting vertical temperature structure of the upper layer of the sea and also on the upwelling and sinking of water in the central part of the east coast of India. Chacko (1950), dealing with the seasonal variations of the planktonic organisms around Krusadai, has also given some hydrographical data of the area from where the plankton collections were made. Ganapati & Murthy (1953) made observations on the distribution and seasonal variations of surface salinity and temperature off the Visakhapatnam coast between latitudes 17° 03.0′N to 17° 41.0′N and 83° 18.2′E to 83° 57.6′E.

MATERIAL AND METHODS

The observations in the present paper are based on 42 plankton samples collected from 33 stations during a series of 12 oceanographic cruises organized by the Andhra University under the general direction of Prof. E. C. La Fond, the visiting professor of Oceanography, during the period October 1952 to March 1953. Though the area of investigation covered most of the western part of the bay from Trincomalle in the south to the Sunderbans in the north, we have for the present confined our observations to the waters off Visakhapatnam extending between Latitude 17° 03.0′N to 17° 40.5′N and 83° 03.0′E to 83° 40.5′E. The cruises were made on minesweepers placed at the disposal of the Andhra University by the Indian Navy from time to time. The stations have been so selected that they represent a profile of the coast for a distance of about 30 miles, the shelf itself extending up to 25 miles on this coast. The area under review is divided into six zones each of 5 miles extent.

A locally made ½ metre plankton net of white organdy was used for the collection of the surface plankton. The net was hauled for approximately the same time at all stations. The plankton from the deeper layers was collected by a closing net made of bolting silk. This net approximately measures ½ metre in diametre and 7′ in overall length. A weight is attached to the cod end of the net when it is lowered down and when it is hauled up to the required depth it is closed by sending down a messenger. The plankton immediately after collection was transferred into a clean glass bottle and preserved in 5% formalin. The sample was diluted in all cases to a constant volume of 500 ml. and the estimations of the total number of diatom cells per ml. were made from aliquot samples. The distances indicated for the different stations are the distances from the nearest point on the shore irrespective of their topographical position with reference to the Visakhapatnam harbour. The locations of the various stations from where the plankton samples were collected are indicated in the chart appended.

Hydrographical Conditions

Visakhapatnam is situated at 17° 44′ N and 83° 23′ E on the eastern coast of India in between the Sacramento shoal to the south and the Orissa coasts to the north. It is surrounded by hilly ranges on all sides and the Eastern Ghats abut into the sea. Consequently the shore is rocky interspersed with sandy patches.

Waltair gets its rainfall both from northeast and southwest monsoons. The southwest monsoon sets in during the latter half of June and prevails till early October. The northeast monsoon commences late in October and continues till December. Waltair gets its maximum amount of rain from the southwest monsoon.

Salinity variations on this coast bear a close resemblance to the conditions observed at Madras. The maximum salinity in the inshore waters is during the period April to May and the minimum during October to November. The average salinity for October in the different 5-mile zones ranged from 18.26% to 26.37% as one passed from inshore to the offshore waters up to a distance of about 30 miles. In December the salinity ranged from 26.00% to 31.49% in waters up to 20 miles off shore. In February there was not much of fluctuation in the salinity in different zones and the range is from 32.82% to 32.95%. In March the range of salinity was from 33.78% to 33.31%., within the 30-mile zone. It is interesting to note that the various zones undergo considerable fluctuations in salinity in the different months. Thus in the first 5-mile zone the salinity of 18.26% in October rises to 26.00% in December, 32.82% in February and 33.78% in March. The salinity fluctuations in the other zones are given in Table I.

The surface temperature of the waters in the various zones was also found to fluctuate along with the salinity. In October the temperature range of the waters within the 30-mile zone is 82.40°F to 84.25°F, the minimum being in the 5- to 10-mile zone, where the salinity is also the lowest. The low salinity and temperature in this zone is obviously due to the prevailing strong southerly current which brings large volumes of fresh water from the rivers in the north. In December the fluctuations in the surface temperature of waters up to 20 miles are very great and the range is from 75.90 to 80.4°F. The lowering of the temperature in the coastal waters during the month is attributed to the general cooling by the atmosphere in this season. The increase both in salinity and temperature in February is due to the inflow along the east coast of a tongue of high saline waters which has an equatorial origin. In March the temperature range is from 79.2° to 81.16°F. The temperature increases from inshore to offshore waters. (Fig. 2.)

The waters in the Bay of Bengal are subjected to two opposite influences, the southwest and northeast monsoons. The northeast coast of India is interesting hydrographically in that most of the large rivers such as the Ganges, the Mahanadi, the Godavari and the Krishna open into the sea on this coast. The large bodies of fresh water brought down by these rivers into the sea influence the salinity and surface temperature of the Bay to a great extent during the different seasons of the year.

There are two opposite currents skirting the coast, a southwesterly current and a northeasterly current. The southwesterly current prevailing from August to November brings in its wake large bodies of fresh water from the mouths of the rivers Ganges, Mahanadi and Irrawadi, which are full after the southwest monsoon. The low salinity and temperature in the 5- to 10-mile zone in October off the coast is obviously the result of this southwest current. This current becomes weakened in the off shore waters in December and consequently the low saline waters are confined to the coast up to 7 miles offshore. This water mass with low salinity, low temperature and high nutrient content influences the marine life on the coast to a great extent. During the middle of December a northeast current becomes established in the Bay and lasts till July. The current brings in high saline waters from the mouth of the bay from the equatorial regions along the eastern coast, which are responsible for the high salinity of the coastal waters during the period December to July.

La Fond (1953), after examining the isotherms in temperature sections taken in the central part of the east coast of India, observed that upwelling of subsurface layers of the sea occurs from March to May, and that sinking of surface layers takes place from September to November.

DISTRIBUTION OF PHYTOPLANKTON

Our previous observations on the inshore plankton of this coast have revealed that though phytoplankton is present throughout the year, there are two maxima, an autumn peak in November and a spring peak in April. We have also observed a succession of major groups of the planktonic organisms viz., diatoms, dinoflagellates and copepods. The autumn bloom owes its commencement to the nutrient materials washed down by the rivers into the sea and brought into the bay in the wake of the southwesterly current. During March to May there is an upwelling in the coastal waters, and this phenomenon is responsible for the commencement of the spring bloom.

Our present investigations have shown that the centre of phytoplankton production on this coast exhibits a regular movement from the offshore to inshore waters from October to December. In October the maximum productivity zone is situated in the 15- to 20-mile zone. This maximum productivity centre moves towards the shore and in November it is situated in the 5- to 10-mile zone. In December the productivity centre is confined to the inshore waters of 0- to 10-mile zone. Along with the movement of the phytoplankton from the offshore to inshore during October to December, the number of phytoplankton cells present in the waters also undergoes a gradual decrease. In October the plankton is distributed over a wide range extending into the oceanic zone and represents the peak of phytoplankton production in the autumn. When the phytoplankton declines quantitatively after the autumn bloom, it becomes more and more restricted to the inshore waters. The reduction in numbers of the phytoplankton is mainly due to the weakening of the southerly current and consequent less production and also perhaps due to grazing by the myriads of invertebrate larvae which appear during these months.

In October the current off the Orissa coast moves in a southerly direction along the Vizag coast with a maximum flow around 16 miles out from the coast. In November there is a distinct decrease in the southerly drift. In December the low saline waters are restricted to the coastal belt extending to about 7 miles offshore, and beyond this zone there is a considerable weakening of the southerly current as evident by the steep rise in the salinity beyond the 10-mile zone. It is interesting to observe that the movement of the centre of phytoplankton production from the offshore to the inshore waters follows the weakening of the southwest current which also takes place in the same direction.

The fact that plankton is not distributed uniformly in the coastal waters of any sea has been generally recognized. The patchiness in the distribution of plankton has been emphasized by Hardy (1936), Hardy and Gunther (1936). This unevenness in the distribution of plankton led Hardy to his first experiments with the continuous plankton recorder. As in other coasts, here also the plankton throughout the area under review presents an unevenness in its distribution. In October out of the three zones that were investigated the 15- to 20-mile zone shows the maximum production of phytoplankton and a minimum productive area is the 25- to 30-mile zone. Similarly in other months also the patchiness of phytoplankton has been observed in various zones.

A study of the vertical hauls, taken in November '52 and March '53, revealed that the subsurface layers up to a depth of 150 or 180 feet were much more productive than the deeper layer. Hauls made from depths 150 to 270 feet contained very few diatoms. In the deeper zone from 270 to 600 feet the phytoplankton was absent. From the foregoing it might be said that the upper 150′ layer is the most productive and that the phytoplankton gradually decreases in number below this depth and are absent below 300′.

Comparing the seasonal variations of phytoplankton on the coasts of Waltair, Madras and Krusadai on the east coast of India one observes a regular succession in the time of commencement of the primary maximum. At Waltair it begins in February, at Madras in March and at Krusadai in June. A similar phenomenon of succession of phytoplankton production is observed on the west coast also. At Trivandrum the primary maximum is from January to May, at Calicut from May to September and at Bombay from September to February. Unlike the east coast the succession of phytoplankton on the west coast is in a south to north direction. It therefore seems that the factor or factors responsible for phytoplankton production move from north to south on the east coast and from south to north on the west coast.

Conclusions

Preliminary observations on distribution of the phytoplankton of this coast indicate that there are two diatom maxima on the coast, an autumn peak in November and a spring peak in April.

There is a tendency for the movement of the diatom maxima from the offshore to the inshore waters from October to December.

The phytoplankton production on this coast is to a large extent influenced by two opposing currents skirting the coast, a southwesterly current from August to November and a northeasterly current from December to July. The southwesterly current brings down large volumes of river water from the mouths of the Ganges, the Brahmaputra, the Mahanadi and the Irrawadi, and this influx of fresh water is responsible for the autumnal diatom bloom. The northeasterly current brings in a tongue of high saline water from the mouth of the Bay and the spring maxima is due to upwelling of the nutrient-laden deeper waters.

It is also interesting to note that there is a regular succession of the commencement of the spring phytoplankton bloom which moves in a north to south direction along the east coast and in a south to north direction on the west coast. The factor or factors responsible for these two opposite movements along the two coasts are not clear.

REFERENCES

1. AIYAR, R. G. MENON, K. S. and MENON, M. G. K. 1936. Plankton records for the years 1929 and 1930. *J. Madras Uni.*, 8, 1-43.
2. CHACKO, P. I. 1950. Marine plankton from waters around the Krusadai Island. *Proc. Ind. Acad. Sci.*, 31, 162-74.
3. DAKIN, W. J. and COLEFAX, A. 1933. The marine plankton of coastal waters of New South Wales. 1. The chief planktonic forms and their distribution. *Proc. Linn. Soc. N. S. Wales.*, 58.
4. GANAPATI, P. N. and MURTHY, V. S. R. 1953. Salinity and temperature variations of the surface waters off the Visakhapatnam coast. *Memoirs in Oceanography*, Andhra University, Waltair. (in press)
5. GANAPATI, P. N. and RAO, C. G. 1953. Observations on the seasonal variations in the phytoplankton production on the Indian coast with special reference to Waltair coast. *Ind. Sci. Cong.*, part III, 184.
6. HERDMAN, W. A. and SCOTT, A. An intensive study of the marine plankton around the south end of the Isle of Man. Report for 1907 on the Lancashire Sea Fisheries Laboratory, 16.
7. JAYARAMAN, R. 1951. Observations on the chemistry of the waters of the Bay of Bengal off Madras city during 1948-49. *Proc. Ind. Acad. Sci.*, 33, 92-99.
8. LA FOND, E. C. 1953. On upwelling and sinking off the east coast of India. *Memoirs in Oceanography*, Andhra University, Waltair. (in press)
9. MENON, K. S. 1931. A preliminary account of the Madras plankton. *Rec. Ind. Mus.*, 33, part IV, 489-516.
10. MURTHY, V. S. R. Studies on the inshore plankton off the Waltair coast. (unpublished).
11. RAGHU PRASAD, R. 1952. Preliminary observations of the temperature gradients and light penetration in the upper 200 feet of waters in the Bay of Bengal. *Ind. Acad. Sci.*, vol. 36, Sec. A, pp. 61-69.

12. Raghu Prasad, R., Rapt, S. V. and Tampi, P. R. S. 1952. Observations on the distribution of plankton at six inshore stations in the Gulf of Mannar. *J. Zool. Soc.*, India, vol. 4, No. 2, pp. 141-151.
13. Sewell, R. B. S. 1913. Notes of the biological work of the R.I.M.S.S. Investigator. *Jour. Asiat. Soc. Beng.*, vol. 9.
14. ———. 1929. Oceanographic and geographic research in Indian waters. *Mem. As. Soc. Bengal*, 9, No. 5, pp. 207-356.

TABLE I

No.	Zone in miles	October 1952			November 1952	December 1952			February 1953			March 1953		
		S%	T°F.	DIATOMS	DIATOMS	S%	T°F.	DIATOMS	S%	T°F.	DIATOMS	S%	T°F.	DIATOMS
1.	0 — 5	18.26	84.05	15062	1083	26.00	75.90	2700	32.82	80.35	—	33.78	79.20	—
2.	5 — 10	17.83	82.40	—	9549	26.36	78.40	2083	32.25	80.90	—	33.31	80.90	383
3.	10 — 15	18.96	84.70	—	—	29.98	79.70	833	32.69	81.03	516	—	—	—
4.	15 — 20	19.84	84.40	25544	—	31.49	80.40	516	32.62	80.85	912	33.22	81.16	616
5.	20 — 25	25.21	82.90	—	—	—	—	—	32.84	80.70	283	—	—	—
6.	25 — 30	26.37	84.25	4383	2466	—	—	—	32.85	80.30	649	33.31	81.00	616

TABLE II

SUMMARY OF OCEANOGRAPHIC OBSERVATIONS

SERIAL No.	STATION No.	DATE	TIME		LAT. N.	LONG. E.	DISTANCE IN MILES	TEMPERATURE AND SALINITY		DIATOMS PER M.L. SAMPLE	DEPTH OF COLLECTION
			FROM	TO				TEMPERATURE °F.	SALINITY %		
1.	15	29 Oct. 1952	1150	1228	17° 37.5′	83° 21.0′	5	82.8	18.78	20166	0′
2.	18		1634	1647	17° 26.0′	83° 31.0′	19	82.9	23.12	36513	0′
3.	32	31 Oct. 1952	1006	1049	17° 03.0′	83° 03.0′	26	82.0	27.78	4383	0′
4.	34		1220	1244	17° 13.0′	83° 04.0′	16	82.2	19.81	14575	0′
5.	36		1500	1515	17° 34.0′	83° 15.0′	3	83.0	—	9958	0′
6.	37	19 Nov. 1952	1135	1205	17° 27.0′	83° 16.5′	9	80.8	27.63	18666	0′
7.	38		1340	1430	17° 07.0′	83° 22.0′	30	81.4	27.57	2466	0′
8.	89	29 Nov. 1952	0935	1016	17° 40.5′	83° 21.7′	3-½	77.9	24.29	1083	0′
9.	89		0935	1016	17° 40.5′	83° 21.7′	3-½	—	—	1533	180-100′
10.	90		1130	1247	17° 37.0′	83° 23.7′	7	81.2	26.65	433	0′
11.	90		1130	1247	17° 37.0′	83° 23.7′	7	—	—	833	180-0′
12.	91	5 Dec. 1952	0754	0810	17° 39.3′	83° 19.5′	2	75.9	26.00	2700	0′
13.	93		0950	—	17° 31.7′	83° 23.7′	10	79.2	27.88	2083	0′
14.	95		1050	1106	17° 28.8′	83° 23.7′	12	80.2	30.64	700	0′
15.	97		1147	1210	17° 26.0′	83° 24.8′	15	80.3	31.83	966	0′
16.	100		1320	1417	17° 22.3′	83° 27.4′	19	79.9	32.25	516	0′
17.	128	19 Feb. 1953	1243	1257	17° 35.7′	83° 22.6′	7	80.9	32.25	366	0′
18.	130		1443	1512	17° 31.3′	83° 27.0′	12	82.1	—	500	0′
19.	132		1608	1618	17° 30.1′	83° 28.7′	15	81.5	—	633	0′
20.	132		1608	1618	17° 30.1′	83° 28.7′	15	—	—	266	210-90′
21.	134		1656	1709	17° 28.2′	83° 29.5′	16	81.5	32.86	1000	0′

TABLE II—*Continued*

Serial No.	Station No.	Date	Time		Lat. N.	Long. E.	Distance in Miles	Temperature and Salinity		Diatoms per M.L. Sample	Depth of Collection
			From	To				Tempera-ture °F.	Salinity %		
22.	135	19 Feb. 1953	1730	1757	17° 26.8′	83° 31.1′	19	—	—	0	360-180′
23.	136		1814	1854	17° 25.4′	83° 32.3′	20	80.5	—	1050	0′
24.	138		1934	2034	17° 21.6′	83° 35.8′	25	80.2	—	300	0′
25.	140		2123	—	17° 17.4′	83° 36.0′	27	79.9	33.04	716	0′
26.	142	20 Feb. 1953	1342	1410	17° 19.0′	83° 36.8′	28	80.7	32.86	866	0′
27.	144		1538	1600	17° 23.9′	83° 29.5′	19	80.7	32.95	1266	0′
28.	173	27 Feb. 1953	0345	0410	17° 08.1′	83° 25.0′	29	80.6	33.13	366	0′
29.	175		0546	0600	17° 15.6′	83° 26.4′	24	80.6	32.75	266	0′
30.	177		0709	0748	17° 20.6′	83° 27.0′	20	80.6	32.77	333	0′
31.	180		0937	1001	17° 29.0′	83° 24.0′	12	80.7	32.65	416	0′
32.	182		1140	1210	17° 34.0′	83° 22.1′	8	80.8	33.04	466	0′
33.	196	4 Mar. 1953	0940	1035	17° 37.7′	83° 22.0′	5	—	—	13833	150-0′
34.	201		1239	1337	17° 34.3′	83° 25.5′	10	80.9	33.31	383	0′
35.	201		1239	1337	17° 34.3′	83° 25.5′	10	—	—	950	180-0′
36.	206		1632	1810	17° 26.6′	83° 33.1′	20	81.16	33.22	616	0′
37.	206		1632	1810	17° 26.6′	83° 33.1′	20	—	—	200	180-0′
38.	206		1632	1810	17° 26.6′	83° 33.1′	20	—	—	283	360-180′
39.	211		2210	0200	17° 19.7′	83° 40.5′	30	81.0	33.31	616	0′
40.	211		2210	0200	17° 19.7′	83° 40.5′	30	—	—	183	150-0′
41.	211		2210	0200	17° 19.7′	83° 40.5′	30	—	—	50	252-150′
42.	211		2210	0200	17° 19.7′	83° 40.5′	30	—	—	0	600-262′

SOME CHEMICAL AND PHYSICAL FACTORS CONTROLLING THE BIOLOGICAL PRODUCTIVITY OF TEMPERATE AND TROPICAL OCEANIC WATERS

By L. H. N. Cooper
Marine Biological Laboratory, Plymouth, England

The Nutrient Balance in the Tropics

Work on the productivity of the sea was initiated in temperate latitudes where winter provides a fallow season. Phosphate, nitrate and silicate build up to the well-known winter maximum and, during the following spring as the days get longer and the sunlight stronger, are consumed by plants. This is a dominant event and has obscured the possible importance of regeneration and immediate and repeated re-use of nutrients during the temperate summer. The rate of turnover of nutrients, in the temperate zones in summer and in the tropics always, is very difficult to establish by chemical analysis (Riley, 1953). A physical approach to the problem of turbulence and light penetration such as that of Riley (1942) or of Sverdrup (1953) is likely to be more effective.

In the tropics the conditions characteristic of the temperate spring never occur, but in some areas near continental slopes fresh supplies of nutrients are introduced by wind-induced upwelling of deep waters which may be seasonal (Currie, 1953).

Many planktonic plants can use ammonia instead of nitrate whilst some prefer it (Harvey, 1940). Others can use organically bound phosphorus such as phytin and glycerophosphate (Chu, 1946).

Under tropical conditions therefore phosphate and nitrate need rarely be regenerated. There will be plants on hand ready to use ammonia and organic compounds of phosphorus and nitrogen as soon as these are set free. Consequently determinations of inorganic phosphate and nitrate may give a misleading picture of potential productivity. The analytical method best capable of providing a ready assessment of potential productivity of tropical waters is probably that for "total" phosphorus introduced by Harvey (1948). It has technical disadvantages, not yet overcome. Even this can give only a better assessment of the balance in hand; it can give no measure of the rate of turnover.

Assessment of Growth Affecting Substances in the Sea

Evidence is accumulating (Lucas, 1947, 1949; Wilson, 1951; Wilson and Armstrong, 1952; Collier *et al.*, 1950) that there are other chemical factors in the sea which affect productivity. Of their nature we as yet know little: we do not even know whether they are inorganic or organic or both. In complete absence of phosphorus and nitrogen compounds nothing can grow but, in presence of a given supply of plant nutrients, the production of organisms may be greatly affected by the presence or absence of substances which favour division of diatoms, fertilization, development and hatching of eggs, development and metamorphosis of larvae and moulting of crustaceans. The biological properties of a water mass depend on the plants and animals that have already lived in the water, enriching it with their metabolites, ('exocrine' substances as suggested by Lucas) and on the presence of muddy bottoms which are more likely to yield quantities of active solutes to the water than are sandy and rocky bottoms. These biological properties are most readily identified by biological assay which, in the first instance, means the recognition of biological indicators of water masses (Russel, 1935, 1939). Under tropical conditions the establishment of characteristic indicator species should prove very profitable not only to the biologist but to the chemist who may then select suitable assay organisms for assessing chemical growth affecting substances.

Means of Enrichment of Tropical Oceanic Surface Waters by Nutrients

Upwelling of deeper, nutrient-richer waters to compensate coastal surface waters driven off shore by regular monsoon or trade winds is a well-established feature of certain tropical areas. Powerful currents swirling past island groups, such as the Galapagos, also enrich the surface waters in the wake of the islands. It is an article of faith amongst some oceanographers that currents passing over deep oceanic submarine banks and ridges should create turbulence in overlying waters but there is little factual evidence in support.

Everywhere when one of the major ocean currents passes over one of the major submarine ridges, even though this may lie at great depth, streamlines will tend to rise bringing nutrient salts nearer to the surface. If current-flow should be non-turbulent, the streamlines, having crossed the bank or ridge, would descend to the original depth. Since some turbulent motion will always be present, some enrichment of surface waters should occur even in fine weather. Vertical mixing processes will be strengthened during periods of strong winds.

In temperate latitudes in the paths of the cyclonic depressions, gales are commonest in winter but may occur at any time of year. Moderate winds are always with us. By contrast, in many parts of the tropics, long spells of quiet weather may be interrupted by infrequent hurricanes, tornados or typhoons which reach velocities never approached by the wind in temperate latitudes. The power of these winds to bring about vertical mixing of the water column must be very great indeed. It would seem that anywhere in the ocean the aftermath of such storms must be a considerable increase in productivity of the surface waters.

Optimum conditions leading to high oceanic productivity should therefore include a combination of winds of hurricane strength with strong currents, impelled by normally regular winds, running over a highly irregular ocean bed. This is a thesis which requires to be established by observation and chemical analysis. It is not an axiom.

Sea Birds as Indicators of Productivity

Sea birds congregate where food is to be had. The several species of petrel show promise as indicators of waters enriched by mid-oceanic upwelling and vertical mixing, though their need to remain within range of their breeding haunts may distort the picture. Around 48°N, 24°W, in the path of the West Wind Drift and immediately to the east of the Mid-Atlantic Ridge, Wilson's petrel is abundant (Unpublished observations by Surgeon-Lieutenant P. Campbell, R.N.V.R., on board H. M. Surveying Ship *Challenger* in 1953; and discussions with Dr. T. J. Hart). It was not seen further eastward of the ridge. It is known to breed only in the Southern Hemisphere and at the opposite season, so that its presence in the North Atlantic in its non-breeding season becomes a promising indication of rich oceanic water.

The Part Played by Heavy Metals

Only nutrients, such as phosphate and nitrate, in true solution in the deeper sea water will be brought up by upwelling over deep submarine ridges. All organisms need small amounts of iron, some need manganese (Harvey, 1947, 1949) whilst the view is strengthening that other heavy metals, such as molybdenum and cobalt (perhaps as Vitamin B_{12}) may be needed by at least some species. Most of the iron in the sea is particulate (Cooper, 1937, 1948) and will tend to sink to the sea bed. The evidence suggests that the supply of iron in the sea is on slow but steady one-way passage from rivers to the ocean bed (Cooper and Vaux, 1949). Over a continental shelf the stock of iron may be used many times but ultimately and remorselessly much is thought to settle on the bed of the abyss. There it stays until geological change raises deep deposits above the level of the sea to renew the cycle of denudation and marine enrichment.

Most heavy metals form sparingly soluble compounds in sea water, though not so sparingly soluble as are the compounds of iron. Many adsorb on solid particles and especially on flocks of ferric hydroxide. There should be a general tendency for the heavy metals in the sea to follow the cycle of iron.

Consequently in areas of oceanic enrichment, though phosphate, nitrate and silicate may be fully adequate for plant and animal production, the slender supplies of available iron and other heavy metals are likely to be limiting.

In igneous rocks copper is less abundant than rubidium, zirconium and other so-called scarce elements (Rankama and Sahama, 1950). It is surprising therefore that it should be sufficiently abundant in the sea to be determinable. More information is needed on its physicochemical behavior, abundance and biological importance in and over deep ocean waters.

A Pattern for Observation and Experiment in Tropical Seas

These ideas influence the pattern of attack on the problems of the productivity of tropical high seas and coastal waters. Requiring examination would seem to be:—

1) The pattern of winds, the persistence and variability of trade winds and monsoons, and the occurrence, frequency, strength and effect on surface enrichment of hurricane, tornados and typhoons over sea areas.

2) The relief of the sea bed, which can be revealed only as echo-sounding traces accumulate and are accurately charted.

3) Until a fairly complete coverage of soundings is available, other means of recognizing richly productive areas may have to be used. Sea birds may be such. Enormous quantities of shoaling tuna are now known to occur in the Pacific far from coasts, suggesting that they are in pursuit of rich food. However, Hart (1953) points out that such large and fast moving animals may perhaps habitually travel long distances without feeding just as whales do. Consequently it needs to be proved that these newly discovered shoals of tuna are in fact feeding. The Kon-Tiki Expedition (Heyerdahl, 1950) found evidence for the wealth of life in the surface waters of the powerful South Equatorial Current far from land. This starts as the Peru Current swinging offshore, but the rich productivity seems to persist for several thousand miles, a quite exceptional event which only a highly irregular bottom seems capable of explaining.

4) The establishment and delimitation of the ocean currents and their variation from time to time.

5) Surveys of the 'upwelling' (*sensu lat.*) of conventional nutrients over rough bottoms. Of these the assay of inorganic phosphate and total phosphorus are easiest to achieve.

6) Surveys of iron and copper throughout the ocean. Both involve technical difficulties, not so much in the laboratory as in the gross risk of contamination from the hydrographic wire and sampling gear.

7) Establishment from amongst the plankton of biological indicators characterizing the various water masses and conditions of upwelling, followed by the attempt to assess what chemical properties of the water the indicators indicate. Hart (private communication) suggests that this is asking too much of indicators which as tentatively recognized at present are far from being precision instruments. They *can* indicate contrasting water masses and *probable* boundary or mixing areas, but so far he would doubt whether the most ardent planktologist would dare to claim more for them. The writer, however, feels that the growth and distribution of organisms in the sea reflects chemical properties of the water which will defy all the skill of the human analyst for some time to come. Any clue which the planktologist can discover is therefore of prime importance to the chemical oceanographer.

8) Quantitative examination of bulk plankton catches, and of indicator species separately, for content of iron, copper and other heavy metals. It is likely that oceanic species require much lower quantities of heavy metals than do coastal and shelf organisms. Spectrographic methods are attractive since they may well reveal differential abundance of elements which at present we do not even suspect of having biological importance. A study of distribution of heavy metals in the whole group of chaetognaths should prove rewarding.

9) The economic motive for such work as this is to catch fish, and amongst those most easily caught are the tuna family. Other pelagic fish, including clupeoids and scombrids, are likely to be abundant, but, for a number of reasons, may not be catchable with conventional drift nets. Not only for commercial exploitation of the smaller pelagic fish but for scientific examination also, some such gear as the Danish two-boat Larsen mid-water trawl (Krason, 1949) or the rather similar Swedish one-boat Larsson trawl (Larsson, 1952) is needed. Such gear needs to be used in conjunction with the echo-sounder and a plankton indicator such as that of Hardy (1936) in both fundamental and economic research.

Areas, where enrichment of the upper waters in mid-ocean is likely, include the Socotra-Chagos Ridge, the Laccadive-Chagos Ridge and the

Seychelles-Mauritius Ridge (Mascarene Ridge or Plateau) in the Indian Ocean, and the San Felix-Juan Fernandez Ridge and the area around the Galapagos Islands in the Pacific.

There is little doubt that there should be an abundance of fish in such areas and the main problem would seem to be to find out how to catch and market them economically. They would need to be 'big ship' fisheries, beyond the present resources of the neighboring countries to explore and develop.

Thus, in tropical surface waters, oceanic and littoral, chemical studies of inorganic nutrients by traditional methods and of heavy metals are sure to advance fundamental knowledge. Such knoweldge is a pre-requisite for a completely scientific attack on all problems of tropical fisheries. But, writing as a chemist seated far from the scene, it seems to me that a more direct biological study of abundance and of rate of turnover of pelagic organisms is likely to pay quicker economic dividends and should be prosecuted in parallel with purely economic research on the presence, catchability and marketability of pelagic fish in oceanic regions. The most conspicuous indicators of productive areas should be abundant oceanic birds, and large fish and marine mammals which frequently break surface to be seen from the decks of passing ships. Coincidence of the several lines of evidence is needed. (But see Hart, 1953.)

REFERENCES

CHU, S. P. 1946. The utilization of organic phosphorus by phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. 26, pp. 285-295.

COLLIER, A., RAY, S. and MAGNITSKY, W. 1950. A preliminary note on naturally occurring organic substances in sea water affecting the feeding of oysters. *Science*, Vol. III, pp. 151-152.

COOPER, L. H. N. 1937. Some conditions governing the solubility of iron. *Proc. Roy. Soc.*, B, Vol. 124, pp. 299-307.

————. 1948. The distribution of iron in the waters of the western English Channel. *Journ. Mar. Biol. Assoc.*, Vol. 27, pp. 279-313.

COOPER, L. H. N. and VAUX, D. 1949. Cascading over the continental slope of water from the Celtic Sea. *Journ. Mar. Biol. Assoc.*, Vol. 28, pp. 719-350.

CURRIE, R. 1953. Upwelling in the Benguela Current. *Nature*, Vol. 171, pp. 479-500.

HARDY, A. C. 1936. The ecological relations between the herring and the plankton investigated with the plankton indicator. Part I. The object, plan and methods of the investigator. *Journ. Mar. Biol. Assoc.*, Vol. 21, pp. 147-177.

HART, T. J. 1953. The influence of turbulence and vertical exchanges on plankton production in the sea. *Proc. Eighth Pac. Sci. Cong.*, Vol. III-A, pp. 1165-1169.

HARVEY, H. W. 1940. Nitrogen and phosphorus required for the growth of phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. 24, pp. 115-123.

———. 1947. Manganese and the growth of phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. 26, pp. 562-579.

———. 1948. The estimation of phosphate and of total phosphorus in sea waters. *Journ. Mar. Biol. Assoc.*, Vol. 27, pp. 337-359.

———. 1949. On manganese in sea and fresh waters. *Journ. Mar. Biol. Assoc.*, Vol. 28, pp. 155-164.

HEYERDAHL, T. 1950. The Kon-Tiki expedition. Translated from the Norwegian by F. H. Lyon, London: George Allen and Unwin, 235 pp.

KRASON, W. S. 1949. Floating grawls. *Fishery Leaflet* No. 343 (U. S. Dept. Interior, Fish and Wildlife Service, Washington, D.C., U.S.A.), June 1949, 5 pp.: F.A.O. World Fisheries Abstracts. Vol. I, No. 1, p. 13, (1950).

LARSSON, K. H. 1952. The "Phantom" pelagic trawl. *Fishing News* (London), Nov. 29, 1952, No. 2067, p. 7.

LUCAS, C. E. 1947. The ecological effects of external metabolites. *Biol. Rev.*, Vol. 22, pp. 270-295.

———. 1949. External metabolites and ecological adaptation. Symposia Soc. Exp. Biol., No. III Selective Toxicity and antibiotics, pp. 336-356.

RANKAMA, K. and SAHAMA, TH. G. 1950. Geochemistry, Univ. Chicago Press, xvi—912 pp.

RILEY, G. A. 1942. The relationship of vertical turbulence and spring diatom flowering. *Journ. Mar. Res.*, Vol. 5, pp. 67-87.

———. 1953. Letter to the editor. *Cons. int. l'Expl.* press, *J. du bous.*, Vol. 19, pp. 85-89.

RUSSEL, F. S. 1936. The importance of certain plankton animals as indicators of water movements in the western end of the English Channel. *Cons. int. l'Expl. Mer., Rapp. Ore-Verb.*, Vol. 100, pp. 7-10.

———. 1939. Hydrographical and biological conditions in the North Sea as indicated by plankton organisms. *Journ. du Cons. int. l'Expl. Mer.*, Vol. 14, pp. 171-192.

SVERDRUP, H. V. 1953. On conditions for the vernal blooming of phytoplankton *Journ. du Cons. int. l'Expl. Mer.*, Vol. 18, pp. 287-295.

WILSON, D. P. 1951. A biological difference between natural sea waters. *Journ. Mar. Biol. Assoc.*, Vol. 30, pp. 1-20.

WILSON, D. P. and ARMSTRONG, F. A. J. 1952. Further experiments on biological differences between natural sea waters. *Journ. Mar. Biol. Assoc.*, Vol. 31, pp. 335-349.

THE INFLUENCE OF TURBULENCE AND VERTICAL EXCHANGES ON PLANKTON PRODUCTION IN THE SEA

By T. J. Hart
National Institute of Oceanography
Wormley, Surrey, England

The statement sometimes made or implied that tropical waters are comparatively poor in nutrient salts, and that *therefore* they cannot support a rich plankton is a gross over-simplification of the matter. It is the interaction of at least three vital factors, nutrient concentration, light penetration and the degree of stabilization of the surface layers, that provides (as I see it) a sound working hypothesis to account for the comparative poverty of warm seas *as a whole,* in contrast to the richer plankton of most (not all) temperate and polar waters. Moreover, the plankton of some limited areas in warm seas is exceptionally rich, and this has been known for a very long time, far longer, indeed, than the techniques that now enable us to formulate a plausible explanation of these phenomena. One has only to consider Dr. G. Schott's earlier writing on the great upwelling regions off the western coasts of the continents, or Dr. Brongersma-Sanders' (1948) valuable survey of the literature on that subject, to realize this.

Over vast areas of the warmer seas the data available clearly show that a very strong discontinuity surface persists at a depth of some 60 to 150 meters, primarily as a result of thermal stratification. It is the shallow surface layer above this that seems continually impoverished with regard to dissolved nutrients and plankton though detectable phosphate may be found as high as 40 metres. Below it nutrients may be ample for rich production, but the amount of light energy available for photosynthesis must be greatly diminished (probably to about 25% of its value immediately beneath the surface) before penetrating to the potentially fertile water. As would seem to follow rationally from this, such rich plankton production as is known to occur in warm seas, is limited to times and places where turbulence suffices to break down the thermocline and enrich the upper levels of the euphotic zone with nutrients.

The great upwelling regions: Peru coastal current, Benguela current and Canary current, which show some upwelling activity throughout most of the year except near their equatorial limits, provide the largest areas in which this beneficent influence of turbulence is exerted. Equally important and better known, but more seasonal in its action, is the upwelling region of the California current. Similar effects, perhaps of briefer duration and certainly more strictly tropical in location, are to be found in the areas of "monsoon type" upwelling, as off southern Arabia and some of the coasts of India.

Other sources of the necessary mixing are: eddy action along oceanic current boundaries, vertical water movements due to submarine ridges, islands and shoals and the intermittent action of tropical storms. Concerning these we have much less data (and oceanographers will surely agree that even large-scale upwelling phenomena demand much further study) but their potential importance, decreasing in something like the order given, seems obvious.

The converse conditions characteristic of colder seas show that the interaction of turbulence with light penetration and nutrient supply may be both favourable and unfavourable to plankton production. Prevalence of high winds and low air temperatures, promoting intense vertical mixing of the surface layers in winter, ensures the replenishment of the euphotic zone with nutrients, but combines with lower light intensity to limit production at that season, reducing the amount of time spent within the shallow range above the compensation depth. Professor Sverdrup's recently suggested concept of the "critical depth" has implications for our consideration here. (Sverdrup, 1953).

An extreme example of the adverse effect of turbulence on phytoplankton production occurs in the more northerly Antarctic surface waters in spring and early summer. Here rough weather normally persists long enough to delay any stabilization of the surface layers (and so, the onset of the main diatom flowering) until long after the light has ceased to be a limiting factor in itself, nutrient concentration, exceptionally high throughout, being of minor importance in this instance. Hence a "plankton calendar" several weeks later than in corresponding latitudes in the northern hemisphere. Gran (1932) first drew attention to the important adverse influence of turbulence under these conditions, and it can be most amply confirmed from the data collected during the Discovery Investigations (Hart, 1934, 1942).

In temperate seas more settled weather in spring-time promotes thermal stratification, and this, with increase in light energy and depth of penetration, favours production until the supply of nutrients in the epithalassa is exhausted, or diminished to a level at which it no longer suffices to enable plant production to keep pace with the grazing of zooplankton herbivores. At this point renewed turbulence may again become favourable, just as it usually is in the tropics. Short periods of strong winds in summer, after the "post-maximal decrease" that usually follows the main flowering, very probably help to promote the sporadic series of lesser waves of production which usually follow in temperate seas, culminating in the even less regular autumnal outburst that often precedes the re-establishment of winter conditions.

Many research workers in many countries are of course the source of these generalizations, and it is impossible to make due acknowledgment to all in a paper of this length, but to those especially interested I commend the references in the following sequence of general surveys of the subject, by authors who have themselves made outstanding individual contributions to our knowledge of it: Steuer (1910), Gran (in Murray and Hjort, 1912), Atkins (1926), Harvey (1928), Gran (1932), Harvey (1945) and Sverdrup, Johnson and Fleming (1946).

New techniques and work in new areas make it necessary for one to be always ready to modify such views, but the main features just recapitulated seem (to me) so clear as to afford a sound basis for planning any future efforts to locate highly productive areas in warm seas. Because a high degree of stability of the surface layers persists throughout most of the year in most warm seas, turbulence in its beneficent aspect is to be looked for as the pre-requisite of rich plankton production in them. Conversely in colder waters the reaction of turbulence alternates between favourable and unfavourable with seasonal and other changes. Very rarely we may find examples of the two-way action of this factorial complex in warmer waters. Recent data from the Benguela current region, collected by the National Institute of Oceanography, seem most logically interpreted in this way. (Currie, 1953; Hart, 1953).

The region is known to provide persistent upwelling activity in a rich coastal belt, with great wealth of marine life of all kinds (Cf. Hentschel, 1936). This was well shown by high concentrations of nutrients in the surface layers, and huge quantities of diatoms inshore on both our surveys; in strong contrast to the conditions in the offshore surface waters less directly influenced by upwelling.

Upwelling activity was greatest in spring, when the stability of the epithalassa was very small. Yet the rich inshore plankton was then slightly (but significantly) less abundant than in autumn when it appeared that a temporary slackening of upwelling had permitted the re-establishment of a shallow thermocline. It would seem that maximum development of the phytoplankton succession is only possible when some slight time-lag ensues after the newly upwelled water has reached the surface, but although *extreme* production here was favoured by stability, pronounced turbulence must have immediately preceded it, the high concentrations of nutrients still present in the upper layers clearly prove this point. Moreover, if the upwelling were not seen renewed, this unusual aspect of stability proving favourable, even in a sub-tropical environment, must speedily have been reversed as the nutrients become exhausted, and possibly through the "self limiting action of the heavy phytoplankton crop in cutting down light penetration. We await the publication of further details of Dr. Steemann Nielsen's data on light penetration, gained during the "Galathea" Expedition, with interest enhanced by this last possibility.

The more oceanic offshore surface waters, where the population density was a whole order of magnitude lower throughout, showed the more usual aspect of turbulence favouring production, which was clearly highest during the spring survey. The three-fold increase in stability in autumn was accompanied by the lowest values for microplankton we recorded in this part of the world.

In the search for new plankton-rich areas in warm seas extensive use of the distance thermograph and bathythermograph may save much time and effort, since negative surface temperature anomaly and breakdown of thermocline are the first signs of the necessary turbulence to be looked for. But the observations must be repeated, so as to cover the changes in extent of such potentially valuable areas with time. Incidental biological observations would certainly increase the value of such scouting operations enormously, probably to a point where *some* extra expenditure of time for that purpose would be profitable. For a real understanding of the conditions in such regions, the need for which would become apparent as soon as fishery prospects looked practicable, nothing short of full scale oceanographic observations in repeated series will suffice.

REFERENCES

ATKINS, W. R. G., 1926. A quantitative consideration of some factors concerned in plant growth in water. *Journ. du Conseil Internat. pour l'Explor. de la Mer,* Vol. I, pp. 197-226.

BRONGERSMA-SANDERS, M., 1948. The importance of upwelling waters to vertebrate palaeontology and oil geology. *Verh. Akad. Wet. Amst.,* 2 Sect., Di. XLV. No. 4.

CURRIE, R. I., 1953. Upwelling in the Benguela current. *Nature,* Vol. 171, p. 497.

GRAN, H. H., 1912. Pelagic plant life. In Murray and Hjort, "Depths of the Ocean," London.

————, 1932. Phytoplankton. Methods and problems. *Journ. du Conseil Internat. pour l'Explor. de la Mer,* Vol. VII, pp. 343-358.

HART, T. J., 1934. On the phytoplankton of the South-West Atlantic and the Bellinghshausen Sea, 1929-31. *Discovery Repts*. VIII, pp. 1-268.

HART, T. J., 1942. Phytoplankton periodicity in Antarctic surface waters. *Discovery Repts.* XXI, pp. 261-356.

————. 1953. Plankton of the Benguela current. *Nature,* Vol. 171, p. 631.

HARVEY, H. W., 1928. The biological chemistry and physics of sea water. Cambridge.

————, 1945. Recent advances in the chemistry and biology of sea water. Cambridge.

HENTSCHEL, E., 1936. Allegemeine biologie des Sudatlantischen Wiss. Ergb. Deutschen Atlant. Exped. 'Meteor' 1925-27. Vol. XI.

STEUER, A. D., 1910. Planktonkunde. Berlin and Leipzig.

SVERDRUP, H. U., 1953. On conditions for the vernal blooming of phytoplankton. *Journ. du Conseil Internat. pour l'Explor. de la Mer,* Vol. XVIII, No. 3, pp. 287-295.

SVERDRUP, H. U., JOHNSON, MARTIN W., and FLEMING, RICHARD H., 1946. The oceans, their physics, chemistry and general biology. 2nd Ed. New York.

THE INFLUENCE OF LARVAL SETTLEMENT UPON THE COMPOSITION OF MARINE LEVEL BOTTOM COMMUNITIES

By Gunnar Thorson
Zoological Museum of the University of Copenhagen, Denmark

Recent investigations have shown that level bottom communities parallel to those described from Danish seas by C. G. Joh. Petersen cover large flats of our globe. Different *Venus*-communities, all associated with sandy bottoms in shallow water, are known from East Greenland, from boreal seas, from the Mediterranean, and from the Persian Gulf. Different *Macoma*-communities, always associated with mixed bottoms just below the tidal-zone are known from high-arctic as well as boreal seas, from the Vancouver region in the Pacific, from Mombassa in East Africa, and so on. Similarly, mud-bottom communities with sea-urchins of the *Echinocardium* type and brittle-stars of the *Amphiura-Amphiodia* types as dominants are known from cold-temperate, warm-temperate and tropical seas. The Swedish Expedition working off the coast of Chile a few years ago has found further parallels to these communities (personal communication, still unpublished), and so on.

It, therefore, seems reasonable to find out what the level bottom communities of Petersen actually "stand for." By far the majority of modern marine ecologists agree in regarding these communities as realities and as good *statistical* units. But are they *ecological* units also, and if so, does their ecological relation only comprise an association, 1) between the animals and the substratum in which they lived, or 2) between the different animal species living in the same area, or 3) a combination of both?

Our recent knowledge of the ecology of pelagic larvae may give us some help to solve the urgent question: How a level bottom community is established.

Petersen, stressing especially the mutual relations between the inhabitants of the same bottom areas, believed that larvae of all species ready to settle would passively "rain down" on the level bottom and that a "survival-of-the-fittest-fight" just after the settling would decide which set of species were best adapted for life in each individual community.

In arctic coastal communities such a "raining down" at random of pelagic larvae is excluded, since here the non-pelagic young will hatch on the bottom among their parents. Here the fight among two neighbour-communities may only take place where they are in contact with each other, i.e. along their frontiers.

Already in temperate seas, however, is the majority of all level bottom species recruited by pelagic larvae, and in tropical level bottoms will up to 90 per cent of all species have a pelagic development. This means, provided that Petersen was right, that each level bottom community in temperate and tropical regions is constantly attacked by "parachuters," which have to be counter-attacked by the "home-guard." If so, there will always be areas, where the "home-guard" has weak points. Thus, on the Dogger Bank in the North Sea it regularly occurs that a population of the lamellibranch *Spisula* is totally eaten up before the next generation has settled—and such nude areas deprived of their "home-guard" seem to be most tempting places for "parachuters." If such "parachute-attacks" were the normal mode of recruiting temperate and tropical level bottoms, it might be expected that such "weak points," attacked constantly by foreign larvae throughout hundreds of years, would lead to heavy infiltrations which at the bitter end might terminate in a dissolution of the communities or at least in a very varied mosaic of such communities as compared with the arctic ones.

This is, however, not the case. The nude areas of the Dogger Bank often "lie fallow" for years despite their lack of "home-guard" and despite the herds of foreign larvae actually occurring in the plankton. Other facts have further shown that the tropical level bottom communities, even when examined on a quantitative basis, are as distinct and occur constantly over just as large and continuous bottom flats as do the arctic ones. Thus, *a priori*, the "raining-down-at-random" theory seems hardly to hold good.

The pelagic life of most level bottom larvae, about three weeks on an average, is very hazardous. Fluctuations in temperature, food supply and in the stock of enemies will decide which set of species is going to perish and which to survive to metamorphosis in each season. The species-composition of this surviving stock is very different from year to year, and it is from this set of species that the level bottom communities have to be recruited.

Vertical pumpseries from the Sound between Denmark and Sweden show that most species of larvae concentrate in and are restricted to rather narrow horizontal strata of water, the vertical range of which is often a few metres only. The larvae, extremely sensitive to light, salinity, temperature, and—in crustaceans—even to pressure, stick to the stratum which is most close to fulfill their different demands. Larvae, which when ready to metamorphose, are photo-positive and at the same time resistant to low salinity and varying temperature, will crowd near the surface and will accordingly never get in contact with muddy bottoms in deep water. Larvae, which at the moment of metamorphosis are photo-negative, preferring at the same time high salinity and a stable temperature, will never get in contact with a sandy bottom in quite shallow water.

Thus, out of the number of larval species surviving to metamorphosis, only a selected, often very reduced set of species will get in contact with each type of bottom, and the selection of species for each bottom must take place in accordance with this "principle of existing possibilities."

Douglas Wilson, in a series of remarkable experiments, has shown that the larvae of several polychaetes when ready to metamorphose will critically examine the bottom substratum to which they are exposed to continue the pelagic life for days or even weeks, if the substratum seems less attractive to them. Other scientists have found similar reactions in archiannelids, in some echinoderms and in some more polychaetes.

During such a prolonged larval life these larvae are transported by the current directly over the bottom testing the substratum at intervals. Since such a transport of for instance 1 knot only may carry the larvae about 170 km. per week, their chance to find a right substratum seems fairly good.

Wilson showed that in a glass vessel the larvae may distinguish between different tiny heaps of substratum with a very subtle sensitivity. In nature, the distributional pattern must, however, be much more coarse than in a glass vessel, since in nature the free choice of the larvae will cease at the very moment they contact a soil, which—though relatively unattractive—comprises that minimum quality of attraction which is sufficient to induce them to settle. A larva transported over the bottom cannot neglect a substratum of some attractivity because it cannot know that a 10 km. longer transport might lead it to a bottom which is still more attractive.

The observations of Wilson and others are mainly made in the laboratories. Are they valid also to other groups of invertebrates and under natural conditions?

Erik Smidt, working at all seasons in the Danish Waddensea and familiar with the pelagic larvae coming in with flood-tide at regular intervals, found a long series of large larvae of species which in the adult stages did not occur on the Waddens. When, at the same time, he undertook a most comprehensive and careful study of the microfauna of the bottom (585 quantitative samples), Smidt did not find a single young bottom stage of any of the high-tide larvae mentioned. Only such bottom invertebrates which also as adults inhabited the Waddens, were present as newly settled young in the microsamples examined. This, as far as I am aware, is the first and till now the only proof in nature, confirming the laboratory experiments of Wilson *et al.*

Wilson's and Smidt's observations thus seem to show, that out of the set of larval species which gets in contact with each type of substratum, will only a selected number of species, attracted by the substratum proper, metamorphose and settle, while the rest will continue the pelagic life till they find a substratum which is more attractive to them. We do not know whether the larvae are attracted or repelled by the mineral structure of the soil only or by this in connection with organic substances sedimented among the mineral grains, for instance secretions or excretions of the macrofauna living in the spot. In some *epifauna* species such attraction of larvae by secretions or excretions of adults of their own species seems to be a fact. This is the so-called "gregariousness" known for oysters, balamids and *Spirorbis,* which are all sessile and hermaphroditic and therefore may take advantage of such an attraction.

A similar attraction among *level* bottom invertebrates in fauna seems, however, less reasonable since young, for instance level bottom lamellibranchs settling among dense populations of their own species, are directly known to be competed out, because the adults are more cheap to run.

Having settled on a suitable substratum the young have to take up competition with the adult populations already present there, and a thinning out of an adult population just after it has spawned but before the larvae settle, is highly advantageous to the next generation and, in the long run, to the whole population.

But each bottom area has its predators directly feeding upon the other animals living there. Thus we actually have a "survival-of-the-fittest-fight" within the individual level bottom community, but only among the selected set of species adapted for life in that special community.

The shoaling numbers of young of all groups found in late summer in bottom areas densely covered by voracious brittle-stars clearly show that the settling larvae are unable to avoid the predators living in the substratum which they prefer. But what about the settling *predator*-larvae? Are they attracted by the substratum only or also, maybe preferably, by the presence of their prey?

Carnivorous gastropods like *Natica* (=*Polynices*) and *Nassa* as well as the voracious starfish and brittle-stars are in their pelagic phase dependent on and controlled by the same type of food as are the larvae of their prey, namely phytoplankton. Even metamorphosing larvae of these predators have hardly any urgent need of animal food, since they may prolong their pelagic life after having tested the bottom, and since during this prolongation they will continue to live on a vegetable diet. Furthermore, the ability even in adult starfish to trace their prey by sensory activity is extremely poor. Some starfish are known not to hunt prey till three days after settling, while others and also some *Naticas* are known to settle at the same time as their prey. These facts and several more facts seem to prove that level bottom predators are induced to settle by the substratum and not by the prey living there and which, later on, they are going to hunt.

Thus, competition within a level bottom community will normally take place only among a set of species, the presence and "citizenship" of which, must already from settling be taken for a "fait accompli." In most cases this will mean that all species voluntarily settling there in reasonable numbers will have a fair chance to be found in that same locality also as adults. Their percentual, mutual numbers found shortly after settling may be heavily displaced by predators and by competition before they reach the adult stage, but in the long run a certain stock of all species will attain their full size.

The fact that pelagic larvae of most predators are controlled by the same food as are the larvae of their prey will remarkably influence also the balance between the number of predators and prey on the bottom, i.e. between "supply and demand." Most brittle-stars have, however, a longer life-cycle than most of their prey animals, thus being present in large numbers as adults when a new generation of their prey is settling down, and in such cases it might be expected that such dense populations of brittle-stars might totally "wipe out" certain species of prey. The restriction of the boreo-atlantic *Macoma-baltica* community to depths without brittle-stars (i.e. less than 8–10 m) have probably to be explained in this way. The inhabitants of this community may thrive in preferably sandy as well as preferably muddy bottoms but their growth is very slow. A *Macoma-baltica* will during the first 10 months of its life attain a size of 5 mm at height, being thus still small enough to be ingested by a brittle-star, while such soft-bottom lamellibranchs as *Syndosmya* (=*Abra*) *alba* and *Cultellus pellucidus*, actually thriving among dense herds of ophiurans, attain a length of 9 mm and 17 mm respectively in less than 4 months, being then already too large to be swallowed and being accordingly out of the "danger-zone."

The arms of *Ophiura* and *Amphiura* will, however, on several level bottoms make so dense a network, that it seems surprising that the young of *Syndosmya* and *Cultellus* are able to survive even their first one or two months on the bottom, during which they are still tiny enough to be ingested by brittle-stars.

The explanation is, however, quite simple. Just when the larvae of *Cultellus* and *Syndosmya* and several other species are going to settle, the ophiurans are "loading up" for spawning. Their swelling gonads will totally reduce the lumen of the stomach which will, for one month at least, prevent the brittle-stars from feeding. For the New England brittle-star, *Ophiura brevispina,* it is, furthermore, directly known that a lethargic phase of, say, one month will follow directly after spawning—a month during which the brittle-stars will be quite apathetic and will hardly take any food at all. If this proves to be the case in other ophiurans too, and observations seem to support this conjecture, this means that a "passive period" sets in for the brittle-stars just at the time when the bottom among them is whorling with newly settled young of all kinds. When, finally, the brittle-stars have regained their appetite most of these young prey animals have grown to such a size that they may no more be ingested by the predators.

Such passive, inactive periods among dominating level bottom predators have hitherto been neglected by science, though they may deeply influence the species-composition of all communities. These passive periods of predators help to explain the fact that in most cases, a species which has settled voluntarily on a level bottom will hardly be fully "wiped out," and accordingly, the species-composition, though fluctuating much as to the number of individuals, will roughly be the same among the adults as among the newly settled young in the same bottom area.

In most cases the final species composition of a level bottom community is just given at the moment when the larvae settle there for life, which again means that the structure and composition of the substratum are the most essential single factor influencing the composition of a level bottom community.

PRESENT STATUS AND FUTURE DEVELOPMENT OF OCEANOGRAPHY *

By Richard H. Fleming
University of Washington Department of Oceanography
Seattle, Washington, U.S.A.

Introduction

Among those engaged in the ancient and rewarding profession of teaching, it is often said that "the best way to learn about a subject is to have to teach it." To this I can heartily subscribe, and it is from the vantage point of the professor's podium that I am going to review some of the characteristics of oceanography and to indicate ways in which the scientific study of the seas might be fostered and developed.

Oceanography may be defined as the scientific study of the oceans and of their relation to man. This is intentionally stated in very broad terms. The science of the seas is developing rapidly, its content and concepts are changing, and at this stage of its growth it would be foolhardy to attempt to formulate a precise definition. Because it is a young science and because of the various approaches that have been followed by individual investigators, there is no general agreement as to the content and objectives of oceanography. It is, therefore, essential that I state clearly my own point of view. To repeat the definition: "Oceanography is the scientific study of the oceans *and of their relation to man.*" I am sure that there can be little argument about the first phrase, but it is upon the impact of the seas on man that I wish to place particular emphasis. This brief phrase includes all of the innumerable problems of the applications of oceanography. Some of these are obvious and are well recognized; others are more obscure or have not yet received the attention they merit.

Possibly my position will be more clearly defined if I add the following objectives. I believe that it is the broad purpose of oceanography to *understand* the present conditions, to *interpret* past conditions, and to *predict* future conditions. Many of the most fascinating and important tasks of oceanography are in the borderline fields between the study of the present oceans and the interpretation of the geological and biological history of our earth. It is, therefore, obvious that a proper share of our efforts should be directed towards the development of what may be termed paleo-oceanography in order to properly understand the role that the oceans have played in the development and evolution of life, in the earth-shaping processes of erosion and deposition of sedimentary débris, and in the geochemical partition of the elements.

---

* Technical Report No. 20, University of Washington and Office of Naval Research, contract N8onr-520/III, Project NR 083 012. Contribution number 193 from the Department of Oceanography of the University of Washington.

To turn to the other aspect of oceanography, the ability to predict future conditions, it is in this realm that we find most of the practical or economically-important applications of oceanography. We are dealing with many complex processes that are often beyond the grasp of existing theory. Some predictions, such as those for the tides, have been dealt with in a satisfactory way as far as practical needs are concerned, but it must be recognized that our understanding of the actual physical hydrodynamics of the tidal movements is only fragmentary. The development during the last decade of our knowledge of the growth and decay of wind-generated waves is an inspiring example of the progress that can be achieved when there is an urgent need for a method of forecasting.

I have said that I intended to speak to you as a university professor. This implies that I believe in the importance of teaching and formal training in oceanography. The topics just mentioned would appear to fall more properly within the spheres of research and engineering applications. Once more to define my position I should say I feel that formal training, research, and practical applications cannot properly be separated. Teaching without research and regard for application is sterile. Application without training and supporting basic research is self-terminating. Research on the sea without proper knowledge of the subject matter of the science can be wastefully repetitive and neglectful of the important basic problems.

Development of Oceanography

I have defined oceanography as the scientific study of the seas. The question may still exist as to whether or not oceanography has yet achieved the status of an independent science. If we briefly review some of the characteristics of a science, I am sure you will agree that, although it is still young, the science of the seas is an individual field of natural science.

To deserve recognition on its own merits, a science must have developed its unique techniques and its own individual body of knowledge. It is obvious that in the early phases of investigation in a new field the techniques employed are initially those of the older sciences. The unique problems involved in the investigation of the biological, geological, chemical, and physical characteristics of the seas can only be attacked by special devices, and the last seventy-five years have been marked by the development and use of techniques that are peculiarly restricted to such investigations. The sonic depth finder and the GEK (Geomagnetic Electro-Kinetograph) might be cited as examples of what I have in mind.

Just as early techniques are drawn from the established sciences, so the results of early researches published in the existing scientific journals are assimilated into the knowledge of their respective fields. However, the development of individual techniques and the growth and expansion of oceanographic knowledge, journals and other means of publication have been established and have grown to a point where the subject matter has long since outgrown the parent sciences from which oceanography can be traced. The rapid increase in the number of periodicals devoted to contributions in oceanography, as well as the ever-increasing number of individual volumes concerning the oceans, offers clear proof that there is now a unique body of knowledge that is not assimilated into the older parent sciences.

To achieve status as an individual science it is obvious that the field must be recognized as a profession; that is, experts in the field must be employed under the title of their specialty. This means that the government, industry, and the public in general must recognize that this is a unique profession. Last but not least, universities and scholars in general must accept the field as worthy of admission to the exclusive ranks of academic subjects appropriate for teaching as well as for research.

Oceanography, in the United States at least, has met all of these requirements and must therefore be prepared to accept the responsibilities as well as the privileges that accompany independence and maturity. These responsibilities involve not only the development of the science in all its aspects but also the broadening of the scope of teaching and research so that students and investigators in other subjects may have the opportunity to glean from the harvest of oceanography those items of particular value to them.

Characteristics of Oceanography

Oceanography always has been and always will be a truly international science. The water masses and the life in the seas recognize no arbitrary man-made boundaries, and the problems that must be dealt with are common to all countries engaged in marine investigations. The oceans are so vast and their problems so complex that satisfactory progress in their study can only be achieved through the combined efforts of all nations.

If the observational data are to be accurate, easily understood, and readily usable, it is obvious that there must be uniform standards of accuracy, uniform methods of analysis, and generally accepted units for reporting of data. The world-wide use of Standard Sea Water (Eau de Mer Normale), prepared in Denmark, as the precise standard for salinity determinations is a classic example of the value of uniform standards. That this service is of importance on an international basis is shown by the fact that it now receives financial support from the United Nations Organization through UNESCO and is sponsored by the International Association of Physical Oceanography. As a step towards the standardization of methods of chemical analysis, treatment and analysis of data, the latter organization also has in preparation a "Technical Handbook on Physical Oceanography."

To further facilitate the exchange of new ideas and techniques and to attain the desirable uniformity in standards and methods, it is essential that there be frequent or continuous contacts between the workers in different countries. With the development of formal teaching and training in oceanography serious efforts should be made to expand the international exchange of faculty members and students. The Pacific Science Association has sponsored scientific meetings for the exchange of techniques and knowledge, and it would seem entirely appropriate for the Association to consider ways and means to promote the exchange of students for periods of training and research. On the agenda for this Congress is a proposal for the establishment of an International Oceanographic Society of the Pacific. There is definite need for such a permanent organization to assist in the development of oceanography in the Pacific, and I trust that it will receive your vigorous support.

The operation of survey and research vessels is a large financial item that is usually beyond the capacity of individual universities and endowed laboratories. It is a historical fact that vessels engaged in extensive programs have always received national or state support. This type of aid is essential and must be provided on a long-term basis. The money and time involved in outfitting, readying, and training a staff for oceanographic work represent a large investment. It is, therefore, poor economy to embark on short-term programs. Furthermore, the day when single cruises will add materially to our knowledge of the sea will soon be past. Emphasis is shifting more and more to the systematic surveys that will provide information on the seasonal variations and year-to-year differences in conditions, and to intensive studies of some particular characteristic of the sea.

There is another aspect of oceanographic work of this type requiring continued and adequate support; that is the analysis, compilation, and publication of the results. Because of the mutual interest of all workers in this material it is of international concern, and it is very gratifying to know that the Pacific Science Association is seeking ways in which to promote such a program for the Pacific.

My remarks have stressed some of the major aspects of oceanography, but it would be grossly misleading if I left you with the impression that only those agencies having large resources in vessels and personnel were capable of making significant contributions to our understanding of the seas. Besides the problem of the open ocean there is a vast array of topics that can be attacked by those with only small vessels, modest laboratory facilities, and limited equipment. The shallow coastal waters, including the intertidal zone, are characterized by extreme variability both in space and time. They also represent the region of concentrated human activity. Partly because of the complexity of the inshore waters and partly because of the romantic lure of the open ocean, very little work has yet been done to establish the physical, chemical, biological and geological characteristics of these shallow waters and to understand the processes that influence them. Systematic observations to learn the character of the annual cycles, studies of spawning and life histories of organisms, investigations of fouling, and analysis of the effects of man-made changes such as dredging or harbor construction are but a few examples of the valuable projects that can be effectively handled by those with limited resources.

For those investigators who wish to concentrate on laboratory work there is always the opportunity to obtain material from the larger organizations, most of whom desperately need assistance in the examination or analysis of samples. The use of models to elucidate the complex phenomena of waves, tides and mixing processes offers innumerable problems for those of an inventive turn of mind. Lastly, there is much that should and must be done to bring together in an integrated form the results of individual cruises or agencies. This geographic approach is one that will bring valuable returns to those with the patience and ingenuity to synthesize the field work of others. Just as all nations with an interest in the seas must participate in oceanographic work, so must all individuals, each contributing to the extent of his opportunities, background, and interests.

Although I do not feel I must justify research and surveys in oceanography, it is desirable to explain why I believe that there should be increased effort devoted to marine investigations. If you accept the premise that oceanographers are concerned not only with the present-day oceans but also with both past and future conditions, then it is possible to see how oceanography has innumerable important applications. In some cases these applications are purely scientific; in other words, the results either are a stimulus to other fields of research or provide information that is essential for the advance of knowledge in such fields. The study of long cores of deep sea sediments is an example; from such cores it is possible to reconstruct certain features of the earth's environment. Because sedimentation in the deep ocean is a continuous but an exceedingly slow process, cores now available represent a condensed history covering at least several million years.

Clues as to the past climates, periods of volcanic activity, and other information that can be gained from such cores are of immediate interest to workers in many fields of science. Such investigations that are of wide interest also tend to attract the attention of other investigators and hence serve the desirable purpose of bringing new techniques and talents to bear on these problems. The petroleum industry has been particularly generous in its support of oceanographic work because of the needs that exist for better understanding of the conditions under which oil-bearing sediments were deposited. This is an example of how studies in a branch of oceanography, namely submarine geology, are of indirect value in the search for petroleum deposits.

We do not have to seek very far to find instances where oceanography is of direct economic value. The numerous projects falling under the general heading of coastal engineering that include harbor design, construction of offshore drilling platforms, the laying of submarine pipelines, etc., all include the requirement for basic knowledge of the environment as well as for engineering data. It is problems of this kind that have focused attention on serious gaps in our understanding of the oceans.

The examples that I have given to illustrate the importance of oceanography have stressed problems in science, technology, and engineering. Actually the oceans exert tremendous influences on our lives, and these often extend far beyond the earth sciences. The design and operation of vessels depend upon an understanding of the characteristics of the seas, and in the realm of hydrography there are many ways in which oceanography can be applied to improve the efficiency and comfort of vessel operations. The currents and winds and waves that affect the ships of today are undoubtedly similar to those that influenced the craft of those who first ventured to sea. Consequently, there are many aspects of the spread of primitive peoples, the history of exploration, and the development of trade routes that should be examined in the light of modern oceanographic knowledge. The differing influences of the relatively benign Mediterranean Sea and the stormy, cold North Atlantic upon the cultures of the races in southern and northern Europe involve students in literature, art, and in the social sciences. The point I wish to emphasize is that there are many facets to the study of the ocean besides those that conventionally constitute the science of oceanography.

THE FUTURE OF OCEANOGRAPHY

The future prospects for oceanography are bright. How rapidly we are able to develop the field depends upon the amount of support provided and upon the number of interested and competent workers in the field. In no other field is there such a deficiency in training as there is in oceanography. Although the opportunities for graduate instruction have been greatly increased since 1940, the demand for personnel has far exceeded the supply. In 1931 I wished to take postgraduate work in oceanography and found that only the Scripps Institution of Oceanography of the University of California provided such opportunities. Today, at least eight universities in the United States offer postgraduate programs leading to degrees in oceanography, and several more provide such training but grant degrees in other departments. Twenty years ago the number of graduate students in training in the United States was less than 10; today the number exceeds 175 (see Appendix).

Although there are eight universities with postgraduate curricula leading to M.S. or Ph.D. degrees in oceanography, there is only one in the United States that provides a major program for undergraduates; that one is the University of Washington. To those concerned with the problems of training in oceanography, it may be of interest to briefly review why the undergraduate program was undertaken.

In an earlier section of this paper I indicated that oceanography now has its own body of techniques, theories, and knowledge. It is obvious that if training is limited to graduate students, they must either spend an abnormal period of time to complete their work or they must concentrate their efforts on some one phase of oceanography. Because of the lack of textbooks, the difficulties in developing laboratory exercises, and the time required for work at sea and the analysis of data, much of the graduate work has tended to be of a theoretical nature. It is obviously desirable that students receive adequate training in all kinds of work, and this can best be accomplished by starting it early in their career. An added reason for beginning their instruction at the undergraduate level is that only in this way can a continuing supply of competent graduate students be developed.

I do not believe that all students should be trained in the same way—if so, it would obviously be most efficient to concentrate all training in a single institution and to have only a single sequence of courses. For those who wish to enter oceanography at the graduate level, there is the opportunity for choice among a number of universities. For those whose interest has crystallized at an earlier stage, there should be opportunities to start their studies in their chosen field. The general background in basic sciences required for postgraduate work in oceanography by virtually all of the universities is such that a graduate in one of the physical or biological sciences is usually required to take additional courses to make up his deficiencies, as well as to take the necessary courses in oceanography. This is another reason why it is desirable for students to have the opportunity to acquire this breadth of training as undergraduates, rather than being required to follow the specialized curricula in other fields.

Obviously, an undergraduate program can only be carried on where the oceanographic department is located on the main campus of a university. There are other advantages to such a situation; for example, graduate students with deficiencies are able to obtain instruction in other departments without interrupting studies in their major field. Equally important are the opportunities for both undergraduate and graduate majors in other departments, such as geology, fisheries, and zoology, to take some courses in oceanography to supplement the training in their major field. Furthermore, there is the opportunity to offer general lower division courses, open to students in any department who have to satisfy a science requirement. The University of Washington offers such a course three times a year, and currently there are about 150 students per year who take it as a general orientation and cultural subject. In training, as in research, each institution has certain unique features, and in developing a general program it is obvious that it must be built up to take maximum advantage of its location, facilities, relation to a university campus, and other factors. The Department of Oceanography of the University of Washington has followed this precept.

It would be pointless to propose any ideal plan for individual oceanographic activities, but it is felt that on a national or regional basis there are opportunities to plan for well-rounded programs of education and training in oceanography. The most important factors are to have the universities aware of the needs for training and to have oceanographers reach general agreement as to the character of training desired and the agencies best situated to give the various programs. This procedure is currently being followed by the Southern Regional Education Board, an organization that includes representatives of the educational agencies in fourteen states in the southeastern part of the United States.

The undergraduate program at the University of Washington is only in its second year, and several years more must pass before it will be possible to determine its strong and weak points. The program does offer many of the advantages listed above, and it is attracting an increasing number of students. If there is any criticism on the part of the students, it is that the curriculum is too difficult. The number of graduate students is also increasing. To date, most of these have not had any previous training in oceanography, and for such students it has been (and will continue to be) necessary to work out individual programs of study so as to provide the breadth of training that is considered to be essential. For those working towards M.S. degrees, emphasis is placed on formal course work with essentially similar programs for candidates for Ph.D. degrees. A thesis is required for the M.S. degree but this is of much smaller scope than the research that will be expected of doctoral candidates.

Our experience to date has already revealed many difficulties in teaching oceanography that are, I am sure, common to all who undertake formal instruction. Among these difficulties are: how to subdivide the subject matter; the proper sequence of subject matter; the coordination of material presented in different courses; the lack of problems and questions for student work; and the lack of laboratory exercises and experiments. Many of these hindrances can be traced to the fact that there are no textbooks on the subject. Although there have been a number of books on oceanography published during the last decade, not one of them is appropriate for undergraduate courses, and even more serious, there are gaps in subject matter that are not covered at all. From our experience so far, I would hesitate to say that the time is yet ripe to publish formal textbooks, but they must be considered as one of the major problems confronting oceanographers concerned with education.

Equally important is the development of the laboratory work. There are obviously many aspects of the techniques of oceanography that are suitable for laboratory instruction, and students should also spend time at sea to learn the field aspects of the work.

The deficiencies are, I believe, in ways to help the student visualize the regional characteristics and the nature of the processes at work in the ocean. The most promising approach to these topics seems to be through the development of models. Some of these may be realistic and have a close correspondence to the natural prototype. As an example, I will mention the dynamic model of Puget Sound that reproduces the tides and tidal currents of the area and that has been used to familiarize students with the character of these phenomena. It is felt, however, that there is a real need for ways to demonstrate such features as the heating and cooling, the deep-sea circulation, internal waves, Coriolis force, etc. In such instances it may be impossible to show realistic models, but the conditions may be simulated in some way so that the student can at least "picture" what is involved.

The examples I have given are all in physical oceanography but there is a similar need in the biological, chemical, and geological aspects of oceanography. Teaching aids are also needed for classroom use. There are no satisfactory large wall charts showing the regional characteristics of the oceans. There is a similar lack in practically all subject matter. In such matters as these, the onus for development must rest on those directly concerned with teaching problems. It is obvious, however, that cooperation, discussion of problems, and exchange of materials on an international as well as on a national scale would be most helpful.

In the earlier sections I mentioned that oceanography must now be treated as a profession. At the present time there is no professional society including all aspects of the science of the seas; furthermore, there are no accepted professional standards. It may be premature to consider what oceanographers with various levels of training should know; however, these are, in large part, the standards that the educator must have in front of him in planning curricula and training programs. It is sincerely hoped that such questions can be discussed at a future meeting of this Congress.

In this paper I have attempted to set before you some concepts as to the nature and present status of oceanography. I have tried to indicate some of the intriguing and perplexing problems that confront us, and the imminent need for the wider recognition of oceanography as a scholarly field for both undergraduate and graduate training. The problems that are involved are of concern to all countries, and I sincerely hope that international agencies such as the Pacific Science Association will continue their interest in such matters.

Attached to this paper is an appendix listing the opportunities for education and training of oceanographers that exist in the United States and Canada. Also included are figures on the number of students in training and those granted degrees during recent years.

APPENDIX *

EDUCATIONAL OPPORTUNITIES FOR OCEANOGRAPHERS IN THE UNITED STATES AND CANADA

Oceanography is the science of the seas and it deals with the oceans in all their aspects. Although individual investigators may concentrate their efforts upon physical, chemical, biological, or geological features of the oceans, the science of oceanography is concerned with the development of a comprehensive point of view. The oceans exert a tremendous influence upon man, and the understanding of their characteristics and processes is essential in order to solve many practical problems. The oceans have played a key role in the geological and biological history of the earth, and it is from a study of the ocean waters, marine life, and the sediments deposited beneath the sea that we must learn how to interpret the story of our planet. Oceanography is a pioneer field, it is young, and the number of investigators is small. Advances in recent years have revealed the value of marine research, and the demand for trained oceanographers has prompted a rapid increase in the number of universities offering formal training in this science. Because the requirements and the nature of the training differ in certain ways from those of the older fields of science and because of the interest of prospective students in the field, this brief review of the educational opportunities has been prepared.

The rapid growth in educational opportunities can be traced to the military demands for oceanographic knowledge that developed during World War II and the shortage of trained oceanographers. Since the termination of the war, government and state agencies have continued to support oceanographic surveys and research and there has been an increasing amount of effort devoted to the oceanographic problems relating to fisheries, coastal engineering, waste disposal, etc. In these problems, industry is providing an increasing amount of financial aid.

It was recognized that full benefit could not be derived from the available funds and facilities unless a proper proportion of effort was devoted to the training of additional personnel. The situation and outlook were clearly stated by Knudsen *et al.* (1950). These authors, after consulting with all interested agencies, outlined a desirable program for the education of oceanographers. Realizing that the individual institutions would meet the situation in different ways, the program was stated in general terms indicating the need for broad training in the basic sciences as well as the nature and amount of course work that should be available in oceanography. Knudsen *et al.* pointed out that it would probably require a minimum of five years' academic work to achieve professional competence in the field. Although no university has adopted the plan in its entirety, it has served as a general objective, each university developing those phases best suited to its individual situation. Additional impetus to the educational program resulted from a survey conducted by the National Academy of Sciences (1952) which was concerned with the need for sustained research productivity.

With the rapid increase in the number of universities involved and the growing number of students who are interested in the science of oceanography, it is of interest to see what the results of the expanded program have been. In the autumn of 1953, inquiries were sent to all universities and research institutions in the United States and Canada that were believed to be offering one or more courses in oceanography. They were asked to provide information about the courses, whether or not degrees were granted in oceanography, the number of students in training, etc. The data received in response to these requests have been summarized in the following tables.

---

* 10 November 1953. Revised 29 December 1953.

Table I lists the universities and other agencies in the United States and Canada that offer one or more courses in oceanography.* Also shown are the number of undergraduate and graduate courses available and whether or not degrees are offered in oceanography or in some basic field of science. Of the twenty-six activities listed:

(a) Eight offer one or more degrees in oceanography.
(b) Six offer degrees in basic science departments with opportunities to take considerable course work in oceanography.
(c) Nine offer one, two or three courses in oceanography for those majoring in the biological or geological sciences.
(d) Three offer opportunities for marine research without any formal courses in oceanography.

It will be seen that, with the exception of the University of Washington and Texas A & M College, all the programs leading to degrees in oceanography are restricted to graduate students. Although many of the universities offer undergraduate courses, these are in most cases limited to "graduate and selected undergraduates" and are intended primarily for graduate students. Several universities offer one general introductory course for undergraduates, but it is only at the University of Washington that a student can take a program satisfying the requirements for an undergraduate major in oceanography. The undergraduate program at Texas A & M College is at present limited to those following a program in meteorology.

The tabulation is as complete as available information warranted; however, the author had to make many arbitrary decisions when compiling the material in Table I. Differences in academic procedures made it difficult to decide where to draw the line between courses in oceanography (that would be included) and those in related fields or basic sciences (that would be omitted). Those universities that have regularly established departments of oceanography were easily dealt with, and only those courses listed by the department were counted. On the other hand, it was difficult to determine the number of courses that should be counted in those universities where some type of "institute" has been established that sponsors programs based on the offerings of other departments. In general, the courses as tabulated exclude seminars, special topic courses, and those designated for student research. In most cases, each course listed is for one semester or for one quarter. The activities have been arranged in the table in a rough geographic sequence for the Atlantic and Pacific areas, reading from north to south.

Table II lists those universities that offer postgraduate training in oceanography and in closely related fields with emphasis on marine sciences. The tabulation shows the size of the teaching staffs and the numbers of graduate students pursuing programs leading to M.S. and Ph.D. degrees in the several subdivisions of oceanography. The final columns show the total numbers of candidates registered in the autumn of 1953.

---

* This listing omits the excellent M.S. program in oceanography provided for Navy aerologists at the U.S. Naval Postgraduate School, Monterey, California.

Table III contains the same universities as in Table II, and the tabulation shows the numbers of M.S. and Ph.D. degrees granted during the past five years. Prior to 1949 the University of California (through the Scripps Institution of Oceanography) was the only university that granted postgraduate degrees in oceanography. Among the remaining ten listed in Table III, it will be noted that the programs are only from one to four years old and that several have not yet granted a single degree. The University of California has so far borne the major burden of training, but a glance at Table II will show that the load is now widely distributed.

The opportunities for training in oceanography can be expected to increase and the number of students to continue to grow. Thus far, the demand for trained personnel has far exceeded the supply, and job opportunities in this field of science are excellent. The work itself is varied and stimulating and provides a productive career for students with an interest and talent for the natural sciences.

Many federal agencies, particularly the U.S. Navy, employ large numbers of oceanographers for both field and office programs. Numerous graduates have been engaged by federal and state agencies to participate in marine fisheries investigations. There are similar opportunities with national, state and local agencies concerned with waste disposal, design of breakwaters and docks, and coastal engineering in general. In recent years there has been an increasing number of opportunities in industry. Petroleum companies have hired many graduates who have specialized in submarine geology, and the industry has called on those with other specialties to assist in designing underwater pipelines and offshore drilling structures such as those built in the Gulf of Mexico. Because of the expansion of survey and research work, many of those granted degrees in recent years have remained with their university or institution to continue working or have joined another activity engaged in similar work or in teaching.

It would be wrong to assume that the science of oceanography has stabilized. The requirements for personnel are still great and the future demand will depend to a large degree upon the capabilities of the individual students and upon the quality of their training. The place and future of oceanography among the other earth sciences have been examined by the Bureau of Labor Statistics (1952). The nature of the duties involved and the opportunities in the federal service are described in the Examination Announcement for Oceanographer (1953).

Programs in oceanography offered by nearly all of the participating universities are restricted to graduate students who are recruited from those whose undergraduate majors have been in such fields as mathematics, physics, chemistry, biology, geology or meteorology. These students have usually followed the curricula stipulated by their major departments, and rarely, if ever, do they have the breadth of training in the basic sciences required for postgraduate work in oceanography. No general pre-oceanography program, designed to provide the desired preparatory training, has been devised. Each university has its own set of prerequisites which differ considerably depending upon the type and variety of courses offered. At a minimum, most students are expected to have had at least a single one-year course in the basic sciences listed above. Very few enter graduate work with such a broad experience and consequently are required to remove deficiencies in these fields as well as carry a heavy program of courses in oceanography. This means that unless they have planned in advance to enter oceanographic work and have acquired a broad background, their graduate program will be extremely heavy. It is therefore obvious that all students contemplating graduate work in oceanography should communicate with the universities of their choice at as early a date as possible in order to determine the best type of preparatory program for them to pursue.

A number of universities offer one or a few courses in oceanography that are open to undergraduates, but only the University of Washington provides a full program leading to the Bachelor of Science degree in oceanography. The objectives of this program are to provide adequate courses in the basic sciences and broad training in the subject matter of oceanography. To achieve professional competence, students will be encouraged to continue beyond the four-year program and will be advised to take additional work in the basic sciences. Candidates for M.S. and Ph.D. degrees who enter the graduate school without previous training in oceanography are expected to remove any deficiencies in the basic sciences and, during the early part of their program, to acquire a broad training in oceanography before they specialize in any one field of the science.

For the convenience of those interested in the educational opportunities in oceanography, the addresses of all activities listed in Table I are given in Table IV.

The information given above shows that oceanography is a vigorous if relatively young science. It should be attractive to those whose interests are directed towards the natural rather than the laboratory sciences. Because it is young, the pattern of training and the job opportunities are varied. It is, therefore, a challenge to those with imagination and ingenuity for it offers innumerable major problems that cannot be solved without the development of new techniques and theories. These problems range from topics in pure research to those in applied oceanography and in oceanographic engineering. The lure of the unknown is always a strong one, and in oceanography there is ample opportunity for the student who wishes to extend the frontiers of knowledge in a pioneer science.

The author wishes to acknowledge the able assistance of Miss M. M. Allan. This study was supported in part by the Office of Naval Research under Contract N8onr-520/III, Project NR 083 012.

TABLE 1

COURSES OFFERED IN OCEANOGRAPHY

PARENT ORGANIZATION	SUBDIVISION RESPONSIBLE	UNDERGRADUATE COURSES							GRADUATE COURSES							DEGREES OFFERED IN OCEANOGRAPHY
		GENERAL	PHYSICAL	CHEMICAL	BIOLOGICAL	GEOLOGICAL	METEOROLOGICAL	PRACTICAL AND FIELD WORK	GENERAL	PHYSICAL	CHEMICAL	BIOLOGICAL	GEOLOGICAL	METEOROLOGICAL	PRACTICAL AND FIELD WORK	
Harvard University	— — — — — — — —	—	—	—	—	—	—	—	—	1	—	1	1	—	—	None
Mass. Inst. of Technology	Dept. of Meteorology	—	1	—	—	—	—	—	—	—	—	—	—	—	—	None
Woods Hole Oceanographic Inst.	— — — — — — — —	—	1	—	1	—	—	—	—	—	—	—	—	—	—	None
Brown University	Dept. of Oceanography	—	3	—	—	—	—	—	—	2	—	—	—	—	—	None (1)
University of Rhode Island	Narragansett Marine Lab.	—	—	—	—	—	—	—	1	—	—	5	—	—	1	M.S. (Biol. Oceanog.)
Yale University	Bingham Oceanographic Lab.	—	—	—	—	—	—	—	1	—	—	—	—	—	—	None (1)
New York University	Dept. of Meteor. & Oceanog.	1	—	—	—	—	—	—	—	7	—	—	—	4	3	M.S. & Ph.D.
Columbia University	Lamont Geological Observatory	No formal courses														None
Cornell University	Dept. of Conservation	1	—	—	—	—	—	—	1	—	—	1	—	—	—	None (2)
U.S. Dept. of Agriculture	Graduate School	—	—	—	—	—	—	—	2	—	—	—	—	—	—	None
Johns Hopkins University	Chesapeake Bay Institute	1	—	—	—	—	—	—	—	6	2	1	1	—	1	M.S. & Ph.D.
College of William & Mary	Virginia Fisheries Lab.	—	—	—	1	—	—	—	—	—	—	—	—	—	—	None
Duke University	Marine Laboratory	1	—	—	—	—	—	—	—	—	—	—	—	—	—	None
University of North Carolina	Inst. of Fisheries Research	No formal courses														None

(1) Degress granted in science departments.
(2) Degrees granted in Department of Conservation.
(3) Numerous courses in Marine Biology and Fisheries.
(4) Ph.D. granted in Zoology and Botany.
(5) B.S. in Meteorology only.
(6) Degrees granted in Zoology and Geology.
(7) Degrees granted in Zoology.

TABLE I—*Continued*

Parent Organization	Subdivision Responsible	Undergraduate Courses							Graduate Courses							Degrees Offered in Oceanography
		General	Physical	Chemical	Biological	Geological	Meteorological	Practical and Field Work	General	Physical	Chemical	Biological	Geological	Meteorological	Practical and Field Work	
University of Miami	Dept. of Marine Sciences	1	—	—	—	—	—	—	3	2	1	(3)	1	—	—	M.S. (3)
Florida State University	The Oceanographic Institute	—	1	—	4	—	—	—	—	1	—	3	—	—	—	M.S. (4)
Texas A & M College	Dept. of Oceanography	1	—	1	—	1	—	—	3	4	2	2	2	2	1	B.S., M.S. & Ph.D. (5)
University of Texas	Inst. of Marine Sciences	No formal courses														None
University of British Columbia	Institute of Oceanography	—	—	—	—	—	—	2	3	4	2	4	—	—	1	None (1)
University of Washington	Dept. of Oceanography	5	3	2	3	2	—	—	2	6	1	2	1	1	1	B.S., M.S. & Ph.D.
College of the Pacific	Pacific Marine Station	—	—	—	1	—	—	—	—	—	—	—	—	—	—	None
Stanford University	Hopkins Marine Station	1	—	—	—	—	—	—	—	—	—	—	—	—	—	None
Univ. of Southern California	— — — — — — — —	—	—	—	—	—	—	—	1	—	—	1	1	—	—	None (6)
University of California	Scripps Inst. of Oceanography	1	3	2	4	2	—	—	1	4	—	—	2	—	—	M.S. & Ph.D.
San Diego State College	Division of Life Sciences	1	—	—	—	—	—	—	—	—	—	—	—	—	—	None
University of Hawaii	Hawaii Marine Laboratory	1	—	—	1	—	—	—	—	—	—	—	—	—	—	None (7)

(1) Degrees granted in science departments.
(2) Degrees granted in Department of Conservation.
(3) Numerous courses in Marine Biology and Fisheries.
(4) Ph.D. granted in Zoology and Botany.
(5) B.S. in Meteorology only.
(6) Degrees granted in Zoology and Geology.
(7) Degrees granted in Zoology.

TABLE II

GRADUATE STUDENTS ENROLLED IN OCEANOGRAPHY AND MARINE SCIENCES AUTUMN 1953

	TEACHING STAFF	DEGREE CANDIDATES						M.S.	PH.D.	TOTAL
		PHYSICAL	CHEMICAL	BIOLOGICAL	GEOLOGICAL	METEOROLOGICAL	OTHER			
Brown University	1	1	—	—	—	—	—	0	1	1
Univ. of Rhode Island	4	—	—	5	—	—	—	5	0	5
New York University	3[a]	4	—	—	—	—	—	0	4	4
Cornell University	1	—	—	2	—	—	—	0	2	2
Johns Hopkins University	4	10	3	—	—	—	—	8	5	13
University of Miami	—	1	—	23	—	—	12[b]	36	0	36
Florida State University	4	2	1	7	—	—	—	6	4	10
Texas A & M College	13	7	3	7	1	7	—	8	17	25
Univ. of British Columbia	4	3	1	4	1	—	—	7	2	9
University of Washington	7	4	4	4	0	2	—	9	5	14
Univ. of Southern Calif.	—	—	—	—	7	—	—	6	1	7[c]
Univ. of California	18	13	4	7	13	—	3[d]	5	35	40
University of Hawaii	—	—	—	12	—	—	—	3	9	12[e]
Totals		45	16	71	22	9	15	93	85	178

a—Total faculty of eight in Department of Meteorology and Oceanography.
b—Fisheries.
c—Geology Department.
d—Biochemistry.
e—Zoology Department.
NOTE:—There are fourteen students pursuing undergraduate programs in oceanography at the University of Washington.

TABLE III

Degrees Granted in Oceanography and Marine Sciences
1949-1953

		1949	1950	1951	1952	1953	Total
Univ. of Rhode Island	M.S.	—	—	5	0	2	7
New York University	M.S.	—	—	—	—	0	0
	Ph.D.	—	—	—	—	0	0
Cornell University	Ph.D.	—	0	0	0	0	0
Johns Hopkins University	M.S.	—	—	1	3	3	7
	Ph.D.	—	—	0	0	0	0
University of Miami	M.S.	—	—	3	4	2	9
Florida State University	M.S.	—	—	2	2	3	7
Texas A & M College	M.S.	—	—	—	3	4	7
	Ph.D.	—	—	—	—	2	2
Univ. of British Columbia	M.S.	—	—	2	2	0	4
	Ph.D.	—	—	0	0	0	0
University of Washington	M.S.	—	—	—	0	0	0
	Ph.D.	—	—	—	0	0	0
Univ. of Southern Calif.*	M.S.	—	—	—	—	—	6
	Ph.D.	—	—	—	—	—	4
University of California	M.S.	8	14	7	12	8	49
	Ph.D.	3	5	6	5	4	23
Total	M.S.	8	14	20	26	22	96
	Ph.D.	3	5	6	5	6	29

* Only cumulative totals available.

Note:—First notation in the columns indicates the year in which the authority was given to grant degrees.

TABLE IV

Addresses of Activities Offering Opportunities for Education and Training in Oceanography

Atlantic Coast:

Harvard University, Cambridge 8, Massachusetts
(Biological Laboratory)
Massachusetts Institute of Technology, Cambridge 39, Massachusetts
(Department of Meteorology)
Woods Hole Oceanographic Institution, Woods Hole, Massachusetts
Brown University, Providence 12, Rhode Island
(Department of Oceanography)
University of Rhode Island, Kingston, Rhode Island
(Narragansett Marine Laboratory)
Yale University, New Haven 11, Connecticut
(Bingham Oceanographic Laboratory)
New York University, New York 53, New York
(Department of Meteorology and Oceanography)
Columbia University, New York 27, New York
(Lamont Geological Observatory, Palisades, New York)
Cornell University, Ithaca, New York
(Department of Conservation)
U. S. Department of Agriculture, Washington 25, D.C.
(Graduate School)
Johns Hopkins University, Baltimore 2, Maryland
(Chesapeake Bay Institute, Annapolis, Maryland)
College of William and Mary, Williamsburg, Virginia
(Virginia Fisheries Laboratory, Gloucester Point, Virginia)
Duke University, Durham, North Carolina
(Duke Marine Laboratory, Beaufort, North Carolina)
University of North Carolina, Chapel Hill, North Carolina
(Institute of Fisheries Research, Morehead City, North Carolina)
University of Miami, Miami, Florida
(Marine Laboratory, Coral Gables 34, Florida)

Gulf Coast:

Florida State University, Tallahassee, Florida
(Oceanographic Institute, Alligator Harbor, Florida)
Texas Agricultural and Mechanical College, College Station, Texas
(Department of Oceanography)
University of Texas, Austin 12, Texas
(Institute of Marine Science, Port Aransas, Texas)

Pacific Coast:

University of British Columbia, Vancouver, B.C.
(Institute of Oceanography)
University of Washington, Seattle 5, Washington
(Department of Oceanography)
College of the Pacific, Stockton, California
(Pacific Marine Station, Dillon Beach, California)
Stanford University, Palo Alto, California
(Hopkins Marine Station, Pacific Grove, California)

TABLE IV (*continued*)

Addresses of Activities Offering Opportunities for Education and Training in Oceanography

University of Southern California, Los Angeles 7, California
    (Allan Hancock Foundation)
University of California, Berkeley and Los Angeles, California
    (Scripps Institution of Oceanography, La Jolla, California)
San Diego State College, San Diego, California
    (Division of Life Sciences)
University of Hawaii, Honolulu 14, T. H.
    (Hawaii Marine Laboratory, Waikiki Beach and Coconut Island, Oahu)

Bibliography to the Appendix

Bureau of Labor Statistics
1952. Employment Outlook for Earth Scientists. Occupational Outlook Series. Bulletin No. 1050, 38 pp. Available from Superintendent of Documents, U.S. Government Printing Office, Washington 25, D.C.

Examination Announcement for Oceanographer
1953. Announcement No. 4-34-2 (1953). Available from Regional Offices of the U.S. Civil Service Commission and from most first and second class post offices.

Knudsen, Vern O., Alfred C. Redfield, Roger Revelle, and Robert R. Schrock.
1950. Education and Training for Oceanographers. *Science*, Vol. III, p. 700-703. 1950.

National Academy of Sciences (Committee on Oceanography)
1952. Oceanography—1951, a Report on the Present Status of the Science of the Sea. Publication 208. 36 pp. Available from the National Academy of Sciences.

ZOOLOGY

Organizing Chairman: Dean LEOPOLDO B. UICHANCO, College of Agriculture, University of the Philippines, College, Laguna.
Secretary: Dr. SILVERIO M. CENDAÑA, College of Agriculture, University of the Philippines, College, Laguna.

. . . .

RESOLUTION ADOPTED IN THE EIGHTH PACIFIC SCIENCE CONGRESS CONCERNING ZOOLOGY

STANDING COMMITTEES

3. That the Standing Committees on Systematic Zoology and Distribution of Terrestrial Faunas in the Inner Pacific be discontinued and in their place a Standing Committee on Pacific Zoology be established.

November 16, 1953

(First Divisional Meeting: Organizational)

Presiding: Dean LEOPOLDO B. UICHANCO, College of Agriculture, University of the Philippines, College, Laguna.

Secretary: Dr. SILVERIO M. CENDAÑA, College of Agriculture, University of the Philippines, College, Laguna.

PROCEEDINGS

1. Dean UICHANCO welcomed the delegates in his capacity as Organizing Chairman for Zoology.
2. The election of the Chairman of the Division was put before the delegates. Dean Uichanco was nominated and unanimously elected, there being no other nomination.
3. The following were chosen to preside at the subsequent meetings of the Division:
    November 17, 1953—Dean L. B. UICHANCO
    November 18, 1953—Dr. HENRY A. BESS
    November 20, 1953—Dr. M. A. LIEFTINCK
    November 21, 1953—Dr. H. BOSCHMA
4. Dr. C. E. PEMBERTON was appointed Chairman of the Standing Committee on Rules and Resolutions, with authority to select the other members of the Committee.
5. Other matters considered:
    (a) *Dean Uichanco,* in reply to an inquiry by *Dr. Bess* as to whether there was a divisional meeting on Saturday afternoon, November 21, remarked that it was the intention to give the members of the Division opportunity to attend meetings of other divisions.
    (b) *Dr. J. L. Gressitt* requested that his paper, "The Insect Fauna of Micronesia" be read on November 20, instead of on November 21, as scheduled. The request was accepted.
6. Inquiries about trips were made.
    (a) The general trip to Los Baños on November 26, will continue as scheduled. The excursionists in the different divisions are to converge at the College of Agriculture at lunch time.
    (b) *Dean Uichanco* opined that a side trip, if there are enough members interested in a "balut factory", in Pateros perhaps, could be arranged; otherwise, a small one may be visited in Los Baños during the trip on November 26 to the College of Agriculture.

November 17, 1953

Presiding: Dean Leopoldo B. Uichanco, College of Agriculture, University of the Philippines, College, Laguna.
Secretary: Dr. Silverio M. Cendaña, College of Agriculture, University of the Philippines, College, Laguna.

PROCEEDINGS

1. Dean Leopoldo B. Uichanco, Chairman of the Standing Committee on Pacific Entomology, rendered his report orally. He touched on:
   (a) The composition of the Standing Committee on Pacific Entomology.
   (b) Entomological work in the Philippines, where there is a dearth of entomological workers, for the reason that very few young workers have become interested in the subject; entomological work is chiefly on the economic aspect and done chiefly in the University of the Philippines and the Department of Agriculture and Natural Resources; also in the Bureau of Health, and in some private institutions.
2. Because they are more familiar with the activities in their respective areas, summary of Entomological work was requested from workers in other countries:
   (1) Dr. C. E. Pemberton, said that Pacific entomology has advanced fast in the last ten years because the Pacific Science Board, which has its headquarters in Honolulu, has (a) brought together much Pacific material, (b) ample means, and (c) is applying the basic experience in Hawaii to the entire Pacific. He pointed out that emphasis has been on taxonomy and collecting expeditions have been made in Indonesia and Micronesia.
   (2) Dr. W. E. van Steenburgh, speaking of entomological activities in Canada pointed out (a) that Canada is not entirely a very cold country and that the climate is temperate during the fall, spring and summer, so that problems on migratory locust, wireworms, and fruit pests exist, (b) that the Pacific Coast, i.e., British Columbia, is continental, (c) that there are two groups of entomologists in Canada, namely agricultural entomologists (who number about 300), and forest entomologists (who number about 200); (d) that close to 90 per cent of the work in entomology is being done by the Plant

Service, and the rest by the educational institutions; (e) that there are a few entomological societies, and (f) that, because Canadian forests are very extensive so that application of insecticides is not only expensive but also not practical, a long-range program of biological control, in which beneficial insects and viruses are introduced, has been inaugurated.

(3) Dr. Henry Townes, in connection with his work in the Philippines, as FOA entomologist to assist in the control of pests, spoke (a) on his introduction of beneficial insects for the control of the corn borer from the United States; (b) that taxonomic work in the Philippines has been set back because of the destruction of collections, references and notes obtained before the war, and (c) his observation that the older workers here have not generally been very active in taxonomy and the younger ones as a rule have not "caught" on.

(4) Dr. J. L. Gressitt, on being asked to give a few remarks, said that Dr. Pemberton had touched on most of the points he had in mind; he would, therefore, confine his remarks to his own work. He was working on the taxonomy of the enormous amount of material collected from Micronesia, chiefly by American soldiers; Dr. Townes and Mr. Owen are also doing part of the work.

3. *Scientific papers and discussions.*

a. Mr. F. Q. Otanes, not being present, the reading and discussion of the first paper scheduled for the afternoon was postponed to a later session.

b. Miller, David. Relationship of Entomology to Plant Quarantine. (Dr. Miller being absent and his paper was not received, the title only was read.)

c. Pemberton, C. E. Progress in the Control of Invertebrate Pests in the Pacific Islands. (See abstract on p. 122–123 of Abstracts of Papers).

Dr. Pemberton touched on (1) the setting up in 1947 of the Committee on Insect Control for the Trust Territories, under the authority of which biological control of the rhinoceros beetle of coconut, the *Bronthispa* beetles on palms and the African snail have been attempted and successfully accomplished; (2) other pests of which successful control by introduction of beneficial insects was accomplished were the taro-leaf hopper, *Tarophagus proserpina* (Kirkaldy) in Hawaii, *Adoretus sinicus* Burm. in Guam, the Oriental fruit fly, *Dacus dorsalis*, in Hawaii and Saipan, the blackwidow spider

Lactrodectus geometricus Koch in Kwajelen, and (3) the attempt to control the banana weevil, *Cosmopolites sordidus* Germar on banana in Hawaii, and *Furcaspis oceana* Lindinger on coconut in Saipan.

d. Katznelson, H. Control of Bee Diseases with Sulpha Drugs and Antibiotics. (Abstract on p. 124 of Abstracts of Papers).

The paper was read by Dr. W. E. van Steenburgh in the absence of Dr. Katznelson.

e. Baird, A. B. Biological Control of Noxious Insects and Weeds in Canada. (Abstract on p. 125 of Abstracts of Papers).

In the absence of the author, the paper was read by Dr. van Steenburgh also. Among those touched on were:

(1) Organization of the Canada Biological Control Unit, which is centered in Ontario, with some 25 entomologists and through which imported parasites must pass for quarantine and observation; has lately been paying attention to insect virus diseases also, as well as insects to control weeds.

(2) The introduction of DDT has reduced efficacy of previously effective parasites. In an effort to develop DDT-resistant parasites, a strain of *Macrocentrus* has been developed and is now being distributed.

A lively discussion followed:

Dean Uichanco: Are there tropical insects that have been introduced into Canada?

Dr. van Steenburgh: None.

Dr. Pemberton: With respect to work on the effect of insecticides on biological control, Canada leads the world today. Insecticide application where there are effective parasites should be approached with caution.

Dr. Bess: Are you regulating the use of insecticides?

Dr. van Steenburgh: I would like to cite one or two experiences. In orchard work, as we use insecticides, we found we have to apply more and more (insecticides). In East Canada, after some seven years of study, less application of insecticide is being advocated.

In the control of forest-insect pests, biological control is about the only means used for such extensive areas. The trouble was that there are certain powerful agencies which somehow succeeded in advocating the use of insecticides. In an experimental forest area, it was shown that during the first year, 99% of the budworms were killed by the application of insecticides. In the second generation of the pest, however, it was found that there were as many budworm eggs as before spraying was done, so that in that particular area, the trees must now be sprayed regularly as in orchards to keep down the budworm.

Dean Uichanco yielded the chair to Dr. Henry A. Bess.

f. Tanada, Y. An Annotated List of Infectious Diseases of Insects in Hawaii. (Abstract on p. 126 of Abstracts of Papers).

The paper was read by Dr. Bess in the absence of the author. There followed a lively discussion. Part of the discussion:

Dr. van Steenburgh: What has been keeping the use of diseases on insect pests so slow?

Dr. Bess: There has been a lot of work done during the last 5 years. In California, the spruce butterfly is very successfully kept under control by spraying water solutions in the field. There are certain difficulties, one of which is that the pathogen is scarce when they are needed. The problem is involved.

Dr. van Steenburgh: In the field, the insect carries a complex of viruses. Introduction of new virus may have some effect.

Dr. Bess: There does not seem ground to fear insect diseases. They should be safe.

The session recessed at noon, and resumed at 2:30 in the afternoon, with Dr. Henry A. Bess presiding.

g. Kuwayama, S. Some Features of the Insect Pests of Rice in Hokkaido, a Northern Limit of Rice Culture, in Relation to Recent Developments in Culture Methods. (Abstract on p. 129 of Abstracts of Papers).

The paper was summarized by Dean Uichanco in the absence of the author.

There was a lively discussion on the paper, part of which follows:

Dr. Townes: Did he apply insecticides?

Dr. Pemberton: Does rice mature earlier when broadcast than when transplanted?

Dr. Gapuz: What methods are used (in the Philippines) for controlling rice pests?

Mr. Sison: Spraying insecticides, gathering of eggs, etc.

Dr. Gapuz: Would not the natural enemies get killed by spraying?

Dr. Townes: Some spraying is being done with organic insecticides. Proper timing of spraying should be observed.

Dr. Torres: Can not the time when parasites are least determine the time for spraying of rice?

Dr. Cendaña: This will require observations over a long period of time. Then there is this to consider also—that the distribution of parasites is not uniform throughout in that some areas will show high degree of parasitism at the same time that others have low parasite density.

RELATIONSHIP OF ENTOMOLOGY TO PLANT QUARANTINE

By David Miller
Cawthron Institute, Nelson, New Zealand

PROGRESS IN THE CONTROL OF INVERTEBRATE PESTS IN THE PACIFIC ISLANDS

By C. E. Pemberton
Invertebrate Consultants Committee for the Pacific
Pacific Science Board, National Research Council
Washington, D.C., U.S.A.

Shortly after the United States assumed the administration of the Trust Territory of the Pacific Islands, the U. S. Commercial Company was organized to conduct an economic survey of the Islands in cooperation with the U. S. Navy. An important feature of this survey was the assignment of H. K. Townes, Jr. and R. G. Oakley, U. S. Bureau of Entomology and Plant Quarantine, to investigate insect problems in the territory. This was accomplished during the summer of 1946. Their reports emphasized the presence of serious agricultural pests. In conference between Admiral Louis E. Denfield, High Commissioner of the Trust Territory, and Harold J. Coolidge, then Executive Secretary of the newly formed Pacific Science Board of the National Research Council, it was felt that definite action should be taken to assist island residents in the control of these pests. Accordingly, Admiral Chester W. Nimitz, Chief of Naval Operations, in a letter to the Pacific Science Board, dated 2 May, 1947, requested such action.

Plans were promptly formulated and the Pacific Science Board appointed an Insect Control Committee for Micronesia, later designated the Invertebrate Consultants Committee for the Pacific, consisting of C. P. Clausen, then Chief, Division of Foreign Parasite Introduction, U. S. Bureau of Entomology and Plant Quarantine, Harry S. Smith, then Chairman, Division of Biological Control, University of California and C. E. Pemberton, Principal Entomologist, Experiment Station, Hawaiian Sugar Planter's Association, Chairman. Later, D. B. Langford, then Entomologist for the Trust Territory, was added to the Committee. Consultants consisted of Joseph C. Bequaert, Museum of Comparative Zoology at Harvard College, and E. C. Zimmerman, Associate Entomologist, Experiment Station, Hawaiian Sugar Planter's Association. The personnel has changed from time to time with some additions; but the original members still serve. Mr. Coolidge, now Executive Director of the Pacific Science Board, has worked with the Committee constantly. Effective action could hardly have been accomplished without his aid. E. H. Bryan, Jr., Bernice P. Bishop Museum, acted as Secretary for the first year, to be succeeded by Ernestine Akers, Pacific Science Board. Mr. Bryan prepared a "Bibliography of Publications on the Insects of Micronesia." This compact, annotated and indexed list, covering 540 titles, was mimeographed and has proved to be an essential document for entomologists who have since worked in the area.

The initial meeting of the Committee was held in Honolulu September 30 to October 2, 1947 and one or more meetings have been held annually thereafter. Various projects under the direction of the Committee will be briefly discussed. They were financed primarily by the Office of Naval Research, Washington, D. C., and transportation was largely furnished by the Navy.

Oryctes rhinoceros Linnaeus.—The notorious rhinoceros beetle became established in the Palau Islands about 1912. It is the most serious of all insect pests of the coconut palm and when numerous actually kills the trees. Within a few years after establishment large numbers of coconut palms were eradicated in the Palaus by this pest. Apparently of South Indian origin it has spread eastward through Indo-Malaya to Formosa, the Philippines and on to New Britain. It reached Samoa about 1909, has recently appeared on an island in the Tonga Group, on Wallis Island west of Samoa, and early in 1953 it became definitely established on Viti Levu in Fiji. In Micronesia it is known only in the Palau Islands. Further spread of this beetle offers a serious threat to the vast coconut plantings throughout the tropical Pacific.

Strenuous efforts to control this insect in the Palaus with parasites, predators and disease pathogens have been made. This began with the appointment of T. R. Gardner, U. S. Bureau of Entomology and Plant Quarantine, in October, 1947, to study and introduce into the Palaus certain scoliid parasites of dynastid grubs reported in the Philippines and the Malay Peninsula. The most promising parasite appeared to be *Scolia patricialis* Burmeister subspecies *plebeja* Gribodo. He succeeded in introducing over 100 adults of this species into the Palaus early in 1948. They were liberated in good condition. There is no evidence of establishment but it is still too early to be certain of this.

The genus *Oryctes* is better represented in species in East Africa and Madagascar than in Indo-Malaya. During the summer of 1945, H. W. Simmonds, former Entomologist, Fiji Department of Agriculture, introduced *Scolia ruficornis* Fabricius from Zanzibar into British Samoa for control of the rhinoceros beetle. About 465 adults survived the trip and were liberated. The parasite became established. It is increasing very slowly. This information led the Pacific Science Board to commission Harold Compere, University of California, who was in Africa on other work, to attempt introduction of this parasite from Zanzibar to the Palaus. Mr. Compere made five shipments of adults during November and December, 1947. A total of 95 individuals survived the trip and were liberated. F. X. Williams, Experiment Station, Hawaiian Sugar Planter's Association, was employed to continue the effort. A shipment by him of *Oryctes* grubs parasitized by *Scolia ruficornis* was made from Zanzibar in February, 1948; but the material arrived dead. Dr. Williams then personally conveyed a cage of adult *ruficornis* to the Palau Islands in June, 1948, of which 50 survived the trip and were liberated.

Still a further attempt to establish this parasite in the Palaus was made when R. Tucker Abbott, U. S. National Museum, who was in Africa for the Pacific Science Board on other work, sent a consignment of 100 *ruficornis* adults from Zanzibar to Palau in May, 1950; but all arrived dead. Mr. Abbott returned home via India and Guam the next month and brought with him 75 more of these wasps, of which 30 survived and were liberated in the Palaus.

In a final attempt to establish *Scolia ruficornis* in the Palaus, N. L. H. Krauss, Hawaii Board of Agriculture and Forestry, was sent to East Africa in June, 1951. During the last quarter of the year he sent nine consignments of the parasite to Palau, totaling 600 individuals, mostly females. Of these, 126 arrived alive and were liberated. On August 7, 1953, 20 months after the last liberation, evidence was obtained on the island of Koror by Mr. R. P. Owen, indicating that this parasite has finally become established.

Other attempts towards the biological control of the rhinoceros beetle in the Palau region, include one shipment of the histerid beetle *Placodes ebeninus* Lew. by Mr. Krauss from East Africa, of which 25 arrived safely and were liberated early in January, 1952, and one good consignment of the histerid beetle *Pachylister chinensis* Queng. from British Samoa to Palau, by Simmonds in February, 1952. A month previously Mr. Simmonds, Mr. Owen, Entomologist of the Trust Territory and J. Linsley Gressitt, engaged by the Pacific Science Board, had observed *P. chinensis* in coconut stumps in Samoa associated with *Oryctes* larvae and experimental tests indicated that the histerid and its larvae readily fed on the smaller dynastid larvae. This led to its introduction into Palau.

In addition to the above projects on the biological control of the rhinoceros beetle, the services of Edward A. Steinhaus, University of California, were obtained during May and June, 1951, to permit him to visit the Palau Islands and test strains of the "Milky Disease" *Bacillus popillae* and other pathogens on *Oryctes* grubs. Dr. Steinhaus gave the problem thorough attention; but the results have been inconclusive.

It is still possible that more of the introductions into the Palau Islands will prove successful. Much time must elapse before proof can be established. Meanwhile artificial control measures are being attempted by Mr. Owen that may have a definite effect in reducing the damage to the remaining coconut palms. This work consists in the gradual elimination of dead or dying coconut stumps and trees that furnish the major breeding media.

Essential to the whole project is the need for a thorough understanding of the ecology of the beetle. Dr. Gressitt gave intensive attention to this phase of the problem in the Palau Islands during 1951. Plans are in process for the publication of his elaborate report.

Brontispa mariana Spaeth.—The Mariana Coconut Beetle is considered the most destructive insect pest of the coconut palm in certain of the Mariana Islands, notably Saipan and Rota. It also occurs in some of the Caroline Islands to the south, from whence it was probably carried to the Marianas many years ago. The larvae of this hispid are surface feeders on the young fronds of the palm. Palms can be killed when attack is heavy and long sustained.

The services of W. Harry Lange, Jr., University of California, were obtained in October, 1947, to search for and introduce into the Marianas, natural enemies of this pest. Dr. Lange spent about six months on the project, confining his explorations to the Philippines, Malaya and Java, where the genus *Brontispa* is abundantly represented. He succeeded in introducing into Saipan and Rota the trichogrammatid egg parasite *Haeckeliania brontispae* Ferriere and the eulophid larval-pupal parasite *Tetrastichus brontispae* (Ferriere), both of which were obtained in the Malay Peninsula and Java. Studies in Saipan indicated that both species could be reared on *Brontispa mariana*. Liberations of both species at Saipan and Rota resulted in the establishment of *Tetrastichus brontispae* only. Dr. Lange has published an informative account of his work on this project.

To determine the results of Dr. Lange's introduction of parasites into Saipan and Rota, Richard L. Doutt, University of California, was engaged to make such investigations from July to November, 1948. He found *T. brontispae* well established on both islands. In some collections of material the parasitism amounted to 77 per cent amongst the larvae and 89 per cent in the pupae. It was concluded that such a control gave promise of permitting the coconut palms to grow normally. Dr. Doutt found no evidence of establishment of the egg parasite. The details of his investigations have been published by him.

Achatina fulica Bowdich.—The Giant African Snail began its eastward march over 100 years ago and now occupies many parts of Micronesia and other regions of the tropical Pacific. It feeds voraciously on many plants as well as on dead organic matter. It was one of the first pests requiring attention by the Insect Control Committee of the Pacific Science Board. As it is of African origin, natural enemies on that continent were sought. Dr. Williams was sent to Africa to work on this project, which began in December, 1947. As an essential part of this problem, a study of the ecology of the snail in Micronesia seemed imperative. Dr. Lange concentrated on this subject on the islands of Saipan, Tinian and Rota during October and November, 1947. His work clarified important points on the life history, habits and economic significance of the snail in these areas. He concluded that the African snail "is a definite threat to all types of plants raised for economic purposes." The results of his research have been published.

Dr. Williams visited several parts of East Africa and finally selected the coast near Mombasa as the most promising section for study. His work was concluded in June, 1948. He shipped and brought to Honolulu living specimens of a drilid beetle, whose larvae feed on various snails, the large carabid beetle *Tefflus hacquardi* Chaud. that preys on the giant snail, and the two carnivorous streptaxid snails *Gonaxis kibweziensis* E. A. Smith and *Edentulina affinis* C. R. Boettger. Dr. Williams was of the opinion that the streptaxid snails were important natural enemies of *Achatina* and other snails in East Africa. Dr. Bequaert, who had previously had much field experience in Africa, supported this view. The several predators brought to Honolulu by Dr. Williams were held for study in a quarantined laboratory of the Hawaii Board of Agriculture and Forestry. In order to test the efficiency and habits of the carnivorous snails in the field, Albert R. Mead, University of Arizona, and Yoshio Kondo, Bishop Museum, Honolulu, were engaged in the summer of 1949 first to conduct further ecological studies of the African snail in Pacific areas and then to locate, if possible, an isolated, uninhabited island, infested with *Achatina*, where the streptaxid snails could be liberated for observation under natural conditions. Resulting from this survey the island of Agiguan in the Mariana group was selected.

Then in April, 1950, Mr. R. Tucker Abbott was sent to East Africa to secure living material of the streptaxid snails for liberation on Agiguan. He succeeded in shipping to Guam 545 *Gonaxis kibweziensis.* Of the two streptaxid species this was considered the better. These were transported to Agiguan from Guam by Mr. Owen on June 1 and liberated. About 300 survived the journey from Africa. Mr. Abbott also sent consignments of the *Gonaxis* and *Edentulina* snails to malacologist Kondo in Honolulu about the same time. These have been held in the laboratory by Mr. Kondo for study. He determined that they could be readily reared when fed young *Achatina* and other small snails.

To check the results of the liberation of *Gonaxis* on Agiguan, J. Lockwood Chamberlin, Harvard University, was engaged to visit Agiguan over a year after the liberation was made. Accompanied by Mr. Owen and George D. Peterson, Jr., he visited Agiguan on August 30, 1951, just 14 months after the carnivorous snails had been placed on the island. The *Gonaxis* was found established and spreading, with evidence of considerable destruction of young *Achatina.* However, the predator was neither abundant nor effecting a control.

In view of Dr. Chamberlin's special training in malacology, he was requested to make an ecological study of the snail on a single well infested island in the Marianas, in order to supply additional information, if possible, not already covered in the studies by Dr. Lange, mentioned above. Tinian Island was chosen. Dr. Chamberlin's investigations were made between June 22 and September 7, 1951. Of special interest was his discovery that the snail persistently migrated upwind, with few exceptions, though available food, topography and cover modified such migrations. This phenomenon had not been previously observed for the species. Other interesting data were obtained on the stimuli responsible for the movements of the snail.

A second visit to Agiguan was made by Mr. Kondo and Mr. Peterson in June, 1952. Progress was noted in the development and spread of the *Gonaxis.* It was estimated that this snail then occupied about 10 acres of the island and was composed of about 25,000 individuals. There was no evidence of *Achatina* control at that time. Some years must elapse before the final outcome of this experiment can be determined.

The African snail is approaching pest proportions in Hawaii on the islands of Maui and Oahu. Efforts towards biological control are underway. While Mr. Krauss was in Africa in 1951 shipping parasites of the rhinoceros beetle, he also sent to the Hawaii Board of Agriculture and Forestry 202 *Gonaxis* snails, 72 of the carabid *Tefflus hacquardi* and 35 of *Tefflus carinatus* Klug. Most of the *Tefflus* arrived alive and many of the *Gonaxis.* These have been held in Honolulu where entomologists of the Board of Agriculture and Forestry have reared them and made liberations in the field on Oahu where *Achatina* snails are abundant. It is too early to report results. The large carabid *Tefflus hacquardi* looks promising in the laboratory breeding work. It breeds readily and feeds actively, either as a larva or adult on the giant snail.

Further work on the biological control of the African snail is underway by the Board of Agriculture and Forestry in Hawaii. Through efforts by Mr. Krauss, carnivorous snails of four genera have been imported from Australia and New Caledonia; but the results have been disappointing. The most recent effort is the introduction to Hawaii from Ceylon of *Lamprophorus tenebrosus* Walk. in September, 1952. Called the Indian Glowworm, this large lampyrid has long been known to feed in the larval and adult stages on both young and adults of *Achatina fulica.* Laboratory studies are being conducted at present on the breeding and feeding habits of the lampyrid.

Recent publications, pertinent to the *Achatina* problem have appeared by Bequaert, Williams, Mead and Lange.

Tarophagus proserpina (Kirkaldy).—This delphacid is widespread in the Pacific and can seriously damage taro (*Colocasia esculenta*), an important food plant in the Pacific, because of its edible, starchy, tuberous rootstock. The leafhopper has caused heavy damage in some of the islands of Micronesia. It is well controlled in Java, the Philippines, Hawaii, Fiji and Samoa by an egg-sucking mirid *Cyrtorhinus fulvus* Knight. It was introduced into Hawaii from the Philippines by D. T. Fullaway in 1938. Entomologists of the Hawaiian Sugar Planter's Association sent a consignment of this mirid to Guam on March 31, 1947, in care of Mr. Langford, who made liberations on that island. It became immediately established. From there Mr. Langford moved colonies to the needed areas in the Caroline Islands.

Cosmopolites sordidus Germar.—This weevil is a major pest of bananas in many tropical countries. It is prevalent in Guam and most of the Micronesian islands where bananas are grown. The predatory histerid beetle *Plaesius javanus* Erichson was introduced into Fiji from Java by W. F. Jepson in 1914, where it became well established and helpful in checking the weevil. Through the services of the Fiji Department of Agriculture, 450 *Plaesius* adults were successfully transported to Guam July 22, 1947 and liberated amongst banana plantings where the weevil prevailed. The species multiplies very slowly. A report from Guam in March, 1949, indicated that it was established. In accordance with original plans it will be moved from Guam to other islands where the weevil occurs, as soon as it can be obtained in quantity.

Early in 1948 Mr. Gardner introduced into Koror, Palau Islands, from the Malay Peninsula, 140 adults of the hydrophilid beetle *Dactylosternum hydrophiloides* W. S. M'Leay. This beetle and its larvae are predatory on banana borer larvae in the banana trunks. The result of this introduction has not been checked.

The Oriental Fruit Fly (*Dacus dorsalis* Hendl.).—The Oriental Fruit Fly is believed to have reached Saipan about 1925; but it was not reported in Guam until December 19, 1947, when K. L. Maehler was able to collect and identify it. Having been found in Hawaii the previous year for the first time, vigorous efforts were made during ensuing years to find and introduce parasites from many countries. Many were discovered and introduced into Hawaii, resulting in the establishment of several species and followed by a decided reduction in damage to various fruits grown in the Islands. During 1949, 1950 and 1952, these parasites were sent to Guam where they were released in suitable places. One of these insects was a known parasite of the melon fly *Dacus cucurbitae* Coq., which also occurred in Guam. To date there is no evidence of the establishment of any of the eleven species introduced.

The False Black Widow Spider (*Latrodectus geometricus* Koch).—Though not considered as poisonous as the true Black Widow Spider *Latrodectus mactans* (Fabr.), the False Black Widow Spider closely resembles the more poisonous one and is to be considered an undesirable spider. It was known to occur abundantly in and about buildings on the island of Kwajalein. In Hawaii the eggs of these two spiders are heavily parasitized by the eurytomid *Eurytoma latrodecti* Fullaway. A consignment of this parasite was prepared by entomologists of the Hawaiian Sugar Planter's Association and taken to Kwajalein by Mr. R. P. Owen, who liberated the material on March 18, 1950. A collection of eggs of this spider was made by Mr. Owen on Kwajalein eleven months later. Examination showed that the parasite had become established.

Adoretus sinicus Burm.—The adults of this oriental scarabaeid are defoliators of a great variety of plants. In Feb., 1949, K. L. Maehler reported it in Guam for the first time and by the close of the year it was believed to be the most serious insect pest on that island. It probably invaded the island from Hawaii. In Hawaii it has been very considerably checked by the scoliid *Campsomeris marginella* Klug subspecies *modesta* Sm., an introduction from the Philippines in 1916. During November, 1950 and January, 1951, entomologists of the Hawaiian Sugar Planter's Association, sent consignments of this parasite to Guam, resulting in establishment. It is anticipated that definite benefit will result. Similarly this scoliid was sent from Hawaii to Western Samoa in October, 1952, for control of *Adoretus versutus* Har., a serious defoliator of cacao and other plants. It is too early to know the results.

Furcaspis oceanica Lindinger.—This diaspine scale, known as the Red Coconut Scale, is widely distributed in Micronesia. On the island of Saipan it is particularly injurious. At times the scales are so abundant that the leaves appear as though painted red. During September and October, 1948, Dr. Doutt observed that the scale was comparatively innocuous on some of the Western Caroline Islands and that it was highly parasitized, especially on the island of Ulithi, by an encyrtid wasp that he considered a new species. He immediately introduced this parasite into Saipan, where no parasites of the scale were known. No subsequent investigations have been reported to determine the results of this important introduction. Dr. Doutt has described this encyrtid under the name *Anabrolepis oceanica.*

Icerya aegyptiaca (Dougl.).—Though not of Egyptian origin this *Icerya* was described in 1890 from material taken in Alexandria, Egypt, where it was causing great damage to certain shade trees. It is present in many parts of Micronesia, where it occurs on a number of different plants. Breadfruit (*Artocarpus incisus*) is a favored host plant and in some islands injury by the coccid is so great that this important native food plant cannot thrive. Entomologists have reported observing trees so heavily infested as to be in a dying condition. In the Mariana and Palau Islands the *Icerya* is present but does not occur in destructive numbers. Early in 1947 Mr. Langford determined that a coccinellid on Rota Island was keeping the coccid thoroughly in check and during 1948, K. L. Maehler observed the same ladybird feeding on the *Icerya* on Guam. Specimens of the ladybird were submitted to Mr. Zimmerman for identification, who determined the beetle as *Rodolia pumila* Weise. The most destructive injury to breadfruit trees by this *Icerya* has been noted on Ulithi Atoll in the Western Carolines and also in parts of the Truk group in the Eastern Carolines. It has also been observed in quantity at Kwajalein in the Marshall Islands. In 1947, Mr. Langford transported the *Rodolia* from Rota to the Truk group and liberated good lots of adults and larvae. By September, 1948, control of the *Icerya* had been effected and the trees were reported recovering. Then in June, 1948, he introduced the *Rodolia* from Saipan to Ulithi Atoll and in October, 1949, he took the coccinellid to Kwajalein and a nearby island. In all cases establishment of the ladybird followed and the results have been satisfactory, according to all reports.

Prior to Mr. Langford's discovery of *Rodolia pumila* in the Mariana Islands, entomologists H. S. Pruthi and V. Prabhaker Rao of India, kindly agreed to forward to Guam a *Rodolia* species known to attack *Icerya aegyptiaca* in that country. Three shipments were made early in 1948. The first two failed but the last contained many living adults. Mr. Maehler liberated some on Guam and Mr. Langford placed the balance amongst *Icerya* colonies on Majuro Atoll in the Marshall Islands. No evidence of establishment has been reported. The species of *Rodolia* was not determined.

Lantana camara L.—This prolific shrub is a serious plant pest on a coconut plantation on the island of Ponape in the Eastern Carolines. Several lantana insects that inhibit the growth and reproduction of the plant in Hawaii were introduced into Ponape from Hawaii in August, 1948 and December, 1949. The material was handled by Mr. Langford. By June, 1951, Langford reported the establishment of the tingitid *Teleonemia lantanae* Distant and the tortricid moth *Epinotia lantana* (Busck). Both were well established and materially affecting the plant. The tortricid destroys the tender growing shoots, while the tingitid feeds on the leaves, causing them to dry up prematurely and fall off.

Epilachna philippinensis Dke.—This phytophagus coccinellid is a pest of solanaceous vegetable crops. It was first observed in Guam by Mr. Maehler on November 23, 1948. One effort has been made to effect control with parasites. During September and October, 1950, Herbert Smith, U. S. Bureau of Entomology and Plant Quarantine, with headquarters in Mexico City, sent three large shipments of the tachinid *Paradexodes epilachnae* Ald. to Guam from Mexico, where this fly parasitizes *Epilachna varivestris* Muls. and *E. defecta* Muls. Nearly 10,000 puparia of the tachinid arrived in Guam in good condition and the emerging flies therefrom were liberated. There is no report of establishment.

Insect Survey of Micronesia

Micronesia occupies a vast expanse of the tropical Pacific and is dotted with some 2,400 islands, many of which are greatly isolated. Any program pertaining to the biological control of insect pests in such an area cannot be intelligently conducted without a broad understanding of its insect fauna. Surveys were planned at the initial meeting of the Insect Control Committee for Micronesia in 1947 and during the ensuing five years the major portion of the Territory has been explored by entomologists, resulting in the collection of about 100,000 insect specimens. This material was collected by Phillip Adams, Richard Bohart, Henry Dybas, R. J. Goss, Ira

LaRivers, R. W. Potts and R. L. Usinger. Other entomologists sent out on special problems during the same period also made extensive collections. These were R. L. Doutt, W. H. Lange, T. R. Gardner, J. L. Gressitt, K. L. Maehler and R. P. Owen.

In addition to the above, Henry Dybas, George Bohart and J. L. Gressitt made other collections during the last war, and before the war O. H. Swezey, Z. Ono of Japan, D. T. Fullaway, R. L. Usinger, R. G. Oakley and Y. Kondo had made collections. Added to collections are those made by Townes and Oakley during 1946 and much material assembled by T. Esaki during the period of Japanese occupation of the Trust Territory. Still more material will result from the collections made by N. L. H. Krauss and Dr. Gressitt in 1952 and the expedition of J. F. Gates Clarke during the first quarter of 1953 to the isolated island of Kusaie in the Eastern Carolines.

Dr. Gressitt has been assigned the stupendous problem of coordinating all of the collections, which he estimates to total about 400,000 specimens, and arranging with specialists for study and preparation of manuscripts covering all groups. A grant from the National Science Foundation to advance this work has been received. Plans are underway for the Bernice P. Bishop Museum, Honolulu, to publish all of the manuscripts under the title "Insects of Micronesia." When this work is completed a vast knowledge of the insect fauna of this region, especially with respect to its relationship to other countries of the Pacific, will be available to future workers on many unforeseen problems that will undoubtedly arise.

Quarantine Problems

Though the major efforts of the Invertebrate Consultants Committee for the Pacific have centered on control of pests already established in Micronesia, the Committee has been constantly aware of the great need for the establishment and maintenance of effective plant and animal quarantines within the area and have advised and conferred with the administrative authorities concerned with this vital matter both in Guam and the Trust Territory. During the initial meeting of the Committee on September 30, 1947, it was recommended that no wild species of animal life or disease organism be introduced into Micronesia or Guam without the Committee's approval, that the importation of noxious weeds or other plants and carriers of plant diseases be prohibited, that certain internal and external quarantines be established, and that an experienced Quarantine Officer of the Plant Quarantine Division of the U.S. Bureau of Entomology and Plant Quarantine be assigned, if possible, to draw up a quarantine code for Guam and the Trust Territory and to supervise its enforcement.

Mr. K. L. Maehler was accordingly loaned by the U. S. Bureau of Entomology and Plant Quarantine to undertake this work. With headquarters in Guam he served as Staff Quarantine Officer through 1948 and part of 1949. He prepared a practical program of plant and animal quarantine for Guam and the Trust Territory. It became a legal document in May, 1948, known as Interim Regulation No. 4–48. Mr. Maehler was succeeded as Staff Quarantine Officer on May 16, 1949, by Mr. R. P. Owen, on loan from the U.S. Bureau of Entomology and Plant Quarantine, and on May 1, 1951, Mr. Owen was succeeded by Mr. G. D. Peterson, a Plant Quarantine Officer from the same Bureau. Mr. Peterson assumed full control of all entomological and quarantine work for the island of Guam, while Mr. Owen took over all similar work for the Trust Territory. An imperative duty for the latter was the preparation of revised quarantine regulations specifically designed for the Trust Territory. This was completed and became operative on January 8. 1952. In February, 1953, Mr. Owen reported to the Invertebrate Consultants Committee for the Pacific that the provisions of the regulation were being enforced satisfactorily. This regulation, known as Executive Order No. 23, was signed by the High Commissioner of the Trust Territory of the Pacific Islands on January 7, 1952. The quarantine officers assigned to Guam and the Trust Territory had the approval of and were recommended by the Invertebrate Consultants Committee.

At the fifth annual meeting of the I. C. C. P. it was recommended that an experienced quarantine officer study the quarantine needs of the Ryukyu Islands and draw up suitable regulations thereto. Mr. A. P. Messenger, Chief, Bureau of Plant Quarantine, California State Department of Agriculture, agreed to do this. He spent August and September, 1951, in the Ryukyus conducting a survey of the whole problem. Shortly thereafter he drafted a thorough agricultural plant quarantine law, providing practical regulations for both interior and exterior quarantines. This was submitted to the United States Civil Administration of the Ryukyu Islands. At the request of the I. C. C. P. he later visited the Ryukyus to observe the operation of the newly created plant quarantine organization. He found the system operating efficiently under the control of a Chief Plant Quarantine Officer and twenty-two Inspectors.

Medical Entomology in the Ryukyu Islands

The recommendation of the I.C.C.P. at their annual meeting on Feb. 14, 1952, that a medical entomologist be sent to the Ryukyus to study an eye disease of horses and its relation to suspected insect vectors, resulted in an investigation of the problem by Dr. G. E. Bohart for several months during that year. The disease, which often causes blindness in the horses, is definitely believed to be caused by the irritation resulting from filarial worm infestation of the eye area. Of outstanding importance was the discovery by Dr. Bohart that at least one species of muscid fly, *Musca conducens,* was a carrier of this worm and responsible for spreading the disease. Other flies of the genus *Musca* were not incriminated; but are still held under suspicion. Dr. Bohart has indicated the need for more study on this problem, covering taxonomy of the worm, its distribution in the Ryukyus, clinical, pathological and parasitological investigations and control of the disease.

The Invertebrate Consultants Committee is deeply grateful to the many institutions and individuals who have participated in the problems here reported. It is especially indebted to the administrating officers of the U. S. Navy, the Office of Naval Research, The Trust Territory of the Pacific Islands, and the Military Air Transport Service.

Literature Cited

Bequaert, Joseph C. 1950. Studies in the Achatininae, a Group of African Land Snails. *Bulletin of the Museum of Comparative Zoology at Harvard College* 105(1): 1-216.

Douglas, J. W. 1890. Notes on Some British and Exotic Coccidae (No. 15). *Ent. Month. Mag.* 26: 79-81.

Doutt, Richard L. 1950. Field Studies on the Parasites of *Brontispa mariana* Spaeth. *Proc. Hawaiian Ent. Soc.* 14(1): 55-58.

————. 1950. The Parasite Complex of *Furcaspis oceanica* Lindinger. *Ann. Ent. Soc. Amer.* 43(4): 501-507.

Lange, W. Harry, Jr. 1950. The Biology of the Mariana Coconut Beetle, *Brontispa mariana* Spaeth, on Saipan, and the Introduction of Parasites from Malaya and Java for its Control. *Proc. Hawaiian Ent. Soc.* 14(1): 143-162.

————. 1950. Life History and Feeding Habits of the Giant African Snail on Saipan. *Pacific Science* 4(4): 323-335.

Mead, Albert R. 1950. Comparative Genital Anatomy of Some African Achatinidae (Pulmonata). *Bulletin of the Museum of Comparative Zoology at Harvard College* 105(2): 219-291.

Mead, Albert R. and Kemmerer, Arthur R. 1953. Amino Acid Content of Dehydrated Giant African Snails (*Achatina fulica* Bowdich). *Science* 117(No. 3032): 138-139.

Williams, F. X. 1951. Life History Studies of East African *Achatina* Snails. *Bulletin of the Museum of Comparative Zoology at Harvard College* 105(3): 295-317.

CONTROL OF BEE DISEASES WITH SULPHA DRUGS AND ANTIBIOTICS[1]

By H. Katznelson
Bacteriology Division, Science Service
Department of Agriculture, Ottawa, Canada

The honeybee in common with other forms of life is subject to a variety of diseases caused by forms ranging from viruses to insects. It is susceptible in both larval and adult stages, its congested manner of living being ideal for rapid spread of infection. In consequence bee diseases are responsible for large annual losses of bees, honey and equipment as well as losses due to decreased cross-pollinating effectiveness of colonies. For this reason extensive efforts have been made during the past decade to control the most serious of these diseases with chemotherapeutic agents such as sulphonamides and antibiotics, thus obviating the need for destroying diseased and contaminated material by burning and other drastic treatments. Such control was first achieved by Haseman and Childers (8) of Missouri, who announced in 1944 the successful treatment with sulpha drugs of colonies infected with American foulbrood, perhaps the most serious of bee diseases. Subsequently antibiotics were also tested (7, 9, 13) and both types of drugs applied in efforts to control other diseases as well, such as European foulbrood, Sacbrood and Nosema (2, 14, 15, 17, 25). The results of investigations along these lines, carried out by the Bacteriology Division, Science Service, in co-operation with the Apiculture Division Experimental Farms Service, will be presented in this paper.

American Foulbrood (AFB)

This is a disease of the larvae of the honeybee only, and is caused by a spore-forming organism, *Bacillus larvae*. It is considered as perhaps the most serious of all bee diseases and is found in every part of the world. The unusual resistance of the spores to heat and disinfectants has led to the reluctant acceptance of burning diseased and contaminated material as the most effective means of control, although this is an expensive procedure. Consequently the announcement of a method of control with sulpha drugs (8) which eliminated burning of colonies and contents was of obvious interest to beekeepers everywhere and stimulated an intense search for other agents, including antibiotics and other sulphonamide derivatives, which might be equally, or more effective. The work of Haseman and Childers (8) therefore was followed by that of Johnson (9, 10, 11), Eckert (1, 2), Milne (19, 20) and others (12, 13, 24) all of whom reported favorably on the use of sulpha drugs as a preventive or prophylactic measure but not as a cure, since recurrence of the disease was often observed, especially when feeding of the drug was discontinued or when it was fed carelessly and at the wrong time (1, 9, 10, 11, 20, 24). Early attempts to use antibiotics such as penicillin and streptomycin were, on the whole, not too promising (7, 9, 13).

---

[1] Contribution No. 366 from the Bacteriology Division, Science Service, Department of Agriculture, Ottawa, Canada.

In the studies reported below, the sulphonamides and antibiotics were first tested *in vitro* against several strains of *Bacillus larvae* growing in a fluid medium. This was followed by apiary tests with the more promising compounds. The latter work was carried out by feeding these substances in 50% sugar syrup heavily infected with AFB spores. One gallon of syrup was fed to each colony. Details of these procedures are published elsewhere (12, 15) and the most pertinent data are summarized in Table I. It may be observed that the sulpha drugs were relatively non-toxic to *B. larvae in vitro*, probably because of the presence in the complex growth medium used, of inhibitors for sulpha compounds, such as para-aminobenzoic acid. The antibiotics were much more active, inhibiting growth at dilutions ranging from 1:300,000 for neomycin to 1:100,000,000 for aureomycin. Apiary tests, however, indicated that sulpha drugs gave complete control—the only acceptable criterion for AFB—whereas most of the antibiotics tested did not, in our hands at least. The only exceptions were terramycin and an impure and cheaper concentrate of this antibiotic, terracon, both of which were effective in preventing development of AFB. It is conceivable that increasing the dosage of antibiotics such as neomycin and aureomycin might give complete control. However, the cost of these drugs might well render their use in such amounts prohibitive.

Stability in honey of compounds found to be effective against AFB is obviously of considerable practical importance. It is possibly owing to their instability under conditions prevailing in a hive that antibiotics such as penicillin, neomycin or aureomycin were not completely effective. Three years ago an experiment was begun with three sulpha drugs to determine their stability in honey. Two grams of each compound were mixed separately into 20 pounds of honey, 5 of which were diluted with an equal amount of water, inoculated with AFB spores and fed to a colony of bees. Unmedicated, inoculated honey was fed to another colony as a control. The remaining 15-pound lots of treated honey were stored; 5 pounds were withdrawn each subsequent summer and tested in a similar manner. The data in Table II show that the drugs tested were completely effective even after three years' storage in honey (16). Similar tests are underway with terramycin.

European Foulbrood (EFB)

The etiological agent of this larval disease is not known with certainty, although some investigators (26, 27) consider it to be caused by a lanceolate, coccoid organism, which has not been cultured in artificial media and which has been incorrectly named *Bacillus pluton.* The disease appears to be increasing in the United States and Canada and often does not respond to the standard methods of control such as requeening or increasing the strength of the colonies (3, 21). Sulpha drugs do not appear to be effective against EFB (2, 25).

During the past few years reports from the provinces of Alberta and Saskatchewan have indicated a sharp increase in number of colonies affected by EFB, especially in apiaries where bees are gassed at the end of each year and new packages installed every spring. Experiments were initiated therefore to determine if this disease could be checked by selected antibiotics either by feeding or spraying. The results of certain of these tests, published elsewhere (17), are summarized in Table III. It may be noted that a clean comb placed in infected colonies also became infected (untreated or control series) and that streptomycin and terramycin prevented infection when fed to these colonies. When the antibiotics were sprayed on clean comb prior to insertion into infected colonies, aureomycin was also effective but not chloromycetin. Where infected material was used, in efforts to cure colonies, feeding trials again showed streptomycin and terramycin to be very promising, whereas only aureomycin showed favorable effects when the infected comb was sprayed with these substances.

Sacbrood

This is a virus disease of larvae but is not considered particularly serious although considerable numbers of larvae are frequently killed by it in the spring and early summer (15). Comparatively little work on its control has been done and for this reason efforts were made to do this with two antibiotics, chloromycetin and aureomycin, which have been reported as being effective against certain virus diseases of animals (18). The antibiotics were fed to colonies at the rate of 200 mgm. per gallon of syrup heavily contaminated with crushed infected larvae. Briefly, encouraging results were obtained with chloromycetin in three separate experiments. However, this antibiotic did not appear to cure badly infected colonies. The problem requires further study.

Nosema Disease

Many attempts have been made to control this widespread infectious protozoan disease of the adult honeybee. Sulpha drugs, arsenicals and other antiprotozoan agents as well as many antibiotics have been tested in vain (6, 22, 23). Recently carbarsone (an arsenical) has been reported to inhibit Nosema in caged bees, but it also shortened their life. It did not control the disease when fed to colonies (25). Studies initiated in our laboratories consisted, in general, of feeding various compounds in 60% sugar syrup heavily inoculated with cysts of Nosema to bees in cages (100 per cage); dead bees were removed daily for examination. The presence of cysts of this organism in the epithelial cells of the ventriculus was the criterion of infection. Suitable studies on the toxicity of the various materials used were carried out prior to the work with inoculated sugar syrup. Many substances were tested [2] without success; however, chloromycetin reduced infection from 60 to 48% and sulphaquinoxaline from 69 to about 35% (15). The most promising of all the compounds tested was the antibiotic fumagillin (14) which reduced infection from 76 to 2% when fed at the rate of 1.0 mg. in 30 ml. syrup per 100 bees. Experiments are now underway to control this disease in the apiary, especially in over-wintering colonies. Reports that this is possible have already appeared (4).

Discussion

The control of bee diseases by an ever-increasing array of sulpha drugs and antibiotics offers the beekeeper of today considerable hope. This must be tempered, however, by the realization that the mere feeding or spraying of an effective substance will not necessarily eliminate a disease from an apiary. The nature of the disease, the time of treatment, the stability of the material and the precautions of the beekeeper himself will influence the final outcome of his efforts. For example, none of the compounds shown to control AFB in colonies is sporicidal. Consequently the use of any of these as a chemotherapeutic measure will not destroy spores in honey, pollen stores, in wax, in scale or on any of the hive parts, all of which may disseminate the disease. The beekeeper may overlook this danger and himself be the vector. That these problems are real is evidenced by the many reports of recurrences of the disease when sulpha drugs are used (1, 9, 10, 11, 20, 24).

---

[2] Streptomycin, aureomycin, thiolutin, magnamycin, chloromycetin, atabrine, paludrine, emetine, carbarsone, carbarsone oxide, ceepryn, chiniofon, diodoquin, chloroquine, sulphametazine, sulphaquinnoxaline and fumagillin.

However, in the case of EFB or Sacbrood these difficulties may not be quite so serious since spores are not involved. With Nosema there is again the same problem of disseminating cysts in the apiary as with AFB spores. For these reasons, it may be simpler to control these diseases, rather than attempt to cure infected colonies, by utilizing effective compounds prophylactically. This may be done more effectively in the period of intense brood-rearing (in the spring) than in the period of active foraging (during the honey flow). The compounds may be fed to colonies or sprayed into them depending on the facilities available. Feeding may be more useful in the spring when relatively little nectar or pollen is available and in which case sugar syrup or honey will be used readily. During the honey flow, however, the bees are less likely to use such food; in which case spraying of medicated syrup may prove most effective.

The whole problem of control is of course most serious with AFB, where a single infected cell endangers a colony. Inspectors are empowered to burn an entire colony and contents if they find even one such cell. The situation is not so serious with EFB since it is caused by a non-spore-forming organism and since it is not essential to eliminate the disease completely. If the drug keeps the disease in check until the colony has built up strength to clean the infection out or until the honey flow begins (at which time the disease frequently disappears) it has served its purpose. Substances such as terramycin may be particularly useful in this connection since the results presented above indicate that it may be effective against both AFB and EFB. Recent work in the United States and Switzerland (4, 5) corroborates these results for AFB and EFB although workers in the latter country claim that EFB may recur within a few weeks. The data obtained in our experiments suggest that either streptomycin or terramycin may hold EFB in check for at least 30 days (17).

Various other considerations in regard to the chemotherapy of bee diseases include stability of the compounds tested, their toxicity and their price. Sulpha drugs are more stable and cheaper than antibiotics but they are not effective against EFB, Sacbrood or Nosema. Antibiotics such as streptomycin or terramycin are fairly stable, yet fumagillin, the compound with the greatest promise for Nosema control, is not. It is possible, however, that such substances may be stabilized, or stable, active derivatives prepared. Their cost may be lessened appreciably by use of impure concentrates such as terracon which appears to be as effective as pure terramycin against AFB. Toxicity of these compounds for bees varies considerably; experience in our laboratories has shown that fumagillin is toxic above certain levels. It is obvious therefore that these materials must be used with discretion.

SUMMARY

Penicillin, terramycin and aureomycin were found to be the most potent of the antibiotics tested *in vitro* against *Bacillus larvae* agent of American foulbrood (AFB) of the honeybee.

Only terramycin, and its impure concentrate terracon, completely controlled AFB in the apiary.

Sulphathiazole, sulphadiazine and sulphamethazine were also completely effective, and were found, in addition, to be stable in honey for at least three years.

Chloromycetin showed some promise in controlling Sacbrood.

European foulbrood (EFB) was controlled by streptomycin and terramycin when fed to infected colonies. Under certain conditions aureomycin also was effective but not chloromycetin.

Of the many substances tested for anti-Nosema activity (sulpha drugs, antibiotics and anti-protozoan agents) the antibiotic fumagillin was by far the most promising.

The implications of the above results to the control of bee diseases in the apiary are discussed.

REFERENCES

1. ECKERT, J. E. Use of sulpha drugs in treatment of American foulbrood disease of honeybees. *J. Econ. Ent.,* 40: 41-44. 1947.
2. ———— The treatment of AFB colonies with sulpha. *Gleanings in Bee Culture,* 76: 483, 525. 1948.
3. EDITORIAL. European foulbrood. *Gleanings in Bee Culture,* 78: 433. 1950.
4. GOCHNAUER, T. A. Chemical control of American foulbrood and Nosema diseases. *Amer. Bee J.,* 93: 410-411. 1953.
5. GUBLER, H. U. and ALLEMANN, O. Die Behandlung der Sauerbrut mit Antibiotica. *Schweitz. Bienen-Zeitung,* 75: 526-530. 1952. (In *Biol. Abst.,* 27: No. 26289. 1953.)
6. HALLER, P. H. Prüfung von Nosema-Heilmitteln. *Schweiz. Bienen-Zeitung,* 11: 474-478. 1948.
7. HASEMAN, L. Further studies with sulphathiazole for control of foulbrood. *J. Econ. Ent.,* 41: 120. 1948.
8. HASEMAN, L. and CHILDERS, L. F. Controlling American foulbrood with sulpha drugs. *Univ. Missouri Agr. Expt. Sta. Bull.,* 482. 1944.
9. JOHNSON, J. P. Sulphathiazole for American foulbrood disease of honeybees. Second report. *J. Econ. Ent.,* 40: 338-343. 1947.
10. ———— Sulpha drugs for American foulbrood of honeybees. Third report. *J. Econ. Ent.,* 41: 314-318. 1948.
11. JOHNSON, J. P. and STADEL, R. Sulphathiazole as a medication for American foulbrood disease of honeybees. *J. Econ. Ent.,* 39: 141-144. 1946.

12. Katznelson, H. The influence of antibiotics and sulpha drugs on *Bacillus larvae*, cause of American foulbrood of the honeybee, *in vivo* and *in vitro*. *J. Bact.*, 59: 421-429: 1950.

13. Katznelson, H. and Gooderham, C. B. Sulphathiazole in relation to American foulbrood. *Sci. Agr.*, 29: 340-344. 1949.

14. Katznelson, H. and Jamieson, C. A. Control of Nosema disease of honeybees with fumagillin. *Science*, 115: 70-71. 1952.

15. ———— Antibiotics and other chemotherapeutic agents in the control of bee diseases. *Sci. Agr.*, 32: 219-225. 1952.

16. ———— Note on current studies on the chemotherapy of American foulbrood and on the stability of sulpha drugs in honey. In preparation.

17. Katznelson, H., Arnott, J. A., and Bland, S. E. Preliminary report on the treatment of European foulbrood of honeybees with antibiotics. *Sci. Agr.*, 32: 180-184. 1952.

18. Kirby, W. M. M. Recent trends in antibiotic therapy. *J. Amer. Med. Assoc.*, 144: 233-236. 1950.

19. Milne, P. S. Sulphonamides and American foulbrood disease of bees. *Nature*, 155: 335. 1945.

20. ———— Sulphonamide treatment of American foulbrood. *Agriculture*, 54: 82-87. 1947.

21. Moffett, J. D. European foulbrood. *Amer. Bee J.*, 91: 286-287. 1951.

22. Morgenthaller, D. Heilmittelversuche bei Nosema. *Schweiz. Bienen-Zeitung*, 9: 1-6. 1940.

23. Palmer-Jones, T. Disease of bees in New Zealand. *N.Z. J. Agr.*, 79: 483-486. 1949.

24. Reinhardt, J. F. The sulphathiazole cure of American foulbrood; an explanatory theory. *J. Econ. Ent.*, 40: 45-48. 1947.

25. Report for 1947 of the Chief of Bureau of Entomology and Plant Quarantine. *Gleanings in Bee Culture*, 76: 77. 1948.

26. Tarr, H. L. A. Studies on European foulbrood of bees. III. Further experiments on the production of the disease. *Ann. Appl. Biol.*, 24: 614-626. 1937.

27. White, G. F. European foulbrood. *Bull. U.S. Dept. Agr.*, No. 810. 1920.

TABLE I

INFLUENCE OF SULPHA DRUGS AND ANTIBIOTICS ON *Bacillus larvae in vitro* AND IN THE APIARY

SUBSTANCE TESTED	INHIBITION OF *Bacillus larvae* (AFB)			
	in vitro TESTS [1]	APIARY TESTS [2] EXAMINATION OF COLONIES, DAYS		
		16	32	28
Sulphathiazole	1:1,000	—	—	—
Sulphadiazine	1:1,000	—	—	—
Sulphamethazine	1:1,000	—	—	—
Penicillin	1:5,000,000	+	++	+++
Streptomycin	1:600,000	+	++	+++
Subtilin	1:600,000	++	+++	+++
Chloromycetin	1:600,000	++	+++	+++
Neomycin	1:300,000	—	—	+
Aureomycin	1:100,000,000	—	+	+
Magnamycin		+	++	+++
Terramycin	1:20,000,000	—	—	—
Terracon		—	—	—
Control		++	+++	+++

[1] Dilution of compound causing complete inhibition of growth in fluid media.

[2] All substances were fed to colonies at the rate of 0.5 gm. per gallon sugar syrup except aureomycin and terramycin which were used at the rate of 0.25 gm. per gallon.

—, no disease; + to +++, increasing amount of disease.

TABLE II

CONTROL OF AFB IN COLONIES BY SULPHA DRUGS STORED IN HONEY

DRUG	STORAGE PERIOD OF DRUG (YEARS)			
	0	1	2	3
Sodium sulphathiazole	—[1]	—	—	—
Sulphathiazole	—	—	—	—
Sulphadiazine	—	—	—	—
None	+++	+++	+++	+++

[1] See legend Table 1.

TABLE III

INFLUENCE OF ANTIBIOTICS ON EFB IN CLEAN AND INFECTED COMB IN INFECTED COLONIES [1]

ANTIBIOTIC	TREATMENT OF COMB OR COLONY			
	CLEAN COMB		INFECTED COMB	
	Colony fed	Comb sprayed	Colony fed	Comb sprayed
Streptomycin	0.5	0	0	19.0
Chloromycetin	2.0	2.3	23.0	67.0
Aureomycin	3.0	0	7.0	0
Terramycin	0.6	0	0	16.0
Control	21.0	—	20.0	—

[1] Expressed as average number of infected larvae per comb, thirty days after medication was begun.

BIOLOGICAL CONTROL OF NOXIOUS INSECTS AND WEEDS IN CANADA[1]

By A. B. Baird[2]
Entomology Division, Science Service
Department of Agriculture
Ottawa, Canada

Introduction

Biological control of noxious insects and weeds in Canada has largely followed or paralleled development in the United States, and the two countries have worked almost as one in obtaining material and information as well as in its interchange and utilization. Early entomologists in both countries observed that many of the most injurious insects were of foreign origin and explained their rapid increase in America by the fact that parasites and other natural enemies were rarely imported with the host insects. In his presidential address to the Entomological Society of Ontario in 1878, Dr. William Saunders made special reference to this and suggested the probable value of introducing the missing parasites of introduced pests. In 1882, before Canada had an organized entomological service, Dr. Saunders obtained from Dr. Lintner, entomologist of the New York State Department of Agriculture, a supply of the egg parasite *Trichogramma pretiosum* Ril. (now usually considered *T. minutum* Ril.), which he released to control the imported currantworm, *Nematus ribesii* (Scop.), in Ontario. Interest was greatly stimulated by the outstanding success of the introduction in 1888 of the vedalia, *Rodolia cardinalis* (Muls.), in the control of the cottony-cushion scale, *Icerya purchasi* Mask., in California. Dr. James Fletcher, the first Dominion Entomologist and Botanist, made several attempts to introduce parasites and disease organisms, and, in 1890, he recorded further releases of *T. pretiosum* and introduction of parasites of the Hessian fly, *Phytophaga destructor* (Say), from Europe.

Canadians were made aware of the devastating effects of an insect increasing unchecked by natural enemies when the larch sawfly, *Pristiphora erichsonii* (Htg.), spread like a scourge across the country and in the late 'nineties destroyed the larch stands of Eastern Canada and the eastern United States. This led to the introduction of natural enemies of this pest between 1910 and 1913. The introduction of natural enemies of the brown-tail moth, *Nygmia phaeorrhoea* (Don.), and the gypsy moth, *Porthetria dispar* (L.), was begun during the same period. The first major effort in the planned use of insect parasites and predators centred around these 3 insects, and resulted in the formation of the Natural Control Investigations unit of the Entomological Branch with headquarters at Fredericton, N. B. This group of workers colonized a number of beneficial species and carried out research and observations across Canada on factors affecting the abundance of some 11 species of phytophagous insects over a period of 10 years.

---

[1] Contribution No. 3192, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

[2] Head, Biological Control Unit.

The next stage began with the finding in Ontario of the European corn borer, *Pyrausta nubilalis* (Hbn.), a serious pest of corn, discovered a few years earlier in the New England States. Introduction of parasites from Europe was initiated by the United States and, in 1923, a Canadian laboratory was established at St. Thomas, Ontario, to co-operate in this important development. In 1925, the laboratory was transferred to Chatham, Ontario. Shortly after this the oriental fruit moth, *Grapholitha molesta* (Busck), invaded the Niagara Peninsula from the United States, and the biological control organization was enlarged in 1928 to provide for introduction of natural enemies of this pest. In 1929, the Dominion Parasite Laboratory was established at Belleville, Ontario, with enlarged facilities for work on these and other species. The next important development was made necessary by efforts to control the European spruce sawfly, *Diprion hercyniae* (Htg.): the construction, in 1936, of an air-conditioned quarantine insectary at Belleville. This made possible the safe handling of insect material from any part of the world and also provided facilities for the efficient production of beneficial species for colonization.

In the 40 years since work began on the larch sawfly, 930 million individuals of some 200 species of beneficial insects have been released in Canada to assist in the control of more than 50 noxious species.

Organization and Methods

The organization for biological control of noxious insects and weeds in Canada is centred in the Biological Control Unit of the Entomology Division, Science Service, Agriculture Department. Service is given by this unit in co-operation with other units of the Entomology Division in all phases of biological control of agricultural pests and, with the Forest Biology Division, Science Service, in the use of beneficial insects in control of forest pests. The use of disease organisms in control of forest pests is carried out by the Insect Pathology Laboratory of the Forest Biology Division at Sault Ste. Marie, Ontario.

The Biological Control Unit was established in 1948 with headquarters at Ottawa and laboratories at Quebec, Quebec; Kingston and Belleville, Ontario; and Vancouver, British Columbia. Unit headquarters is responsible for the over-all program of development of biological control in Canada. The Belleville laboratory is the centre for introduction of beneficial insects, for basic research on problems associated with the utilization of these insects, and for their production and colonization. The Kingston laboratory serves as headquarters for work on insect diseases associated with control projects of the Unit. Officers of the Quebec and Vancouver laboratories deal with release and establishment of beneficial organisms in the areas served by them and conduct field research in collaboration with workers of other units. For special assignments, officers from the Unit laboratories are stationed at laboratories of other units and divisions for varying periods as required. Canada has given financial support and various forms of assistance to the Commonwealth Institute of Biological Control throughout the various stages of its development and utilizes the services offered, when advantageous, in obtaining material from foreign countries. For the most part, however, first-hand contacts have proved more satisfactory in obtaining material and information, and two-way co-operation is arranged with as many countries as possible.

The present Unit establishment consists of some 40 research and technical workers with supporting staffs and 50 to 75 seasonal workers, employed chiefly in the summer months. Laboratory facilities are being increased by a modern building now under construction at Belleville, which will provide extensive research laboratories, administrative and office accommodation, and an air-conditioned quarantine wing for insect disease research to which the Kingston pathology section will be transferred. The Belleville laboratory has a field station some 45 acres in extent for development of a number of field research projects, and a summer laboratory is maintained at Parke Reserve, Quebec, for research associated with colonization of parasites of forest pests.

Some Cases of Biological Control in Canada

Larch sawfly, Pristiphora erichsonii (Htg.).—Introduction of parasites of this insect was the first major project in biological control in Canada and one of the most successful, although the methods employed would be frowned upon today. The larval parasite *Mesoleius tenthredinis* Morley has played the most important role, although another larval parasite, *Bessa harveyi* (Tns.) (*B. selecta* (Mg.) of American authors), and a cocoon parasite, *Tritneptis klugii* (Ratz.), have been contributing factors in control in some regions. *M. tenthredinis* was introduced from England during the period 1910 to 1913 and releases were made in central Quebec, eastern Ontario, southern Manitoba, and northern Michigan. Releases were made by having the boxes of imported sawfly cocoons as they came packed in moss from the forest floor in England placed out in infested larch stands, removing the covers, and allowing all emerging insects to escape. Studies in Manitoba showed that between 1913 and 1928 two cycles of sawfly infestation were brought under control by *M. tenthredinis*, and similar successful colonization of this species was noted in Michigan, Ontario, and Quebec. Material from these areas was used to colonize the species in New Brunswick and British Columbia, and distribution has been continued until practically all areas infested by *P. erichsonii* in Canada and the United States have been colonized. In almost all cases where *M. tenthredinis* was released, its rate of increase was such that control was effected in 3 to 5 years. An exception is an area across northwestern Ontario, northern Manitoba, and Saskatchewan, where *M. tenthredinis* persists at a low level of population because of encystment of a large portion of the eggs deposited in the host larvae. It appears that in this area the sawfly infestation may be largely by a species or race other than the normal form of *P. erichsonii*, and the situation is being investigated.

Brown-tail Moth, Nygmia phaeorrhoea (Don.).—During the period 1912 to 1917, 3 parasites, *Apanteles lacteicolor* Vier., *Meteorus versicolor* (Wesm.), and *Compsilura concinnata* (Mg.), were colonized in Eastern Canada following their establishment in the United States. All 3 species proved of great value, the last 2 contributing much in control of the satin moth as well. *C. concinnata* has been recolonized throughout Canada and destroys large numbers of many pest species each year. Attempts were also made to establish the predacious beetle *Calosoma sycophanta* (L.) and the fungous disease *Entomophthora aulicae* (Reichardt ex Bail) Wint., but, so far as known, both were unsuccessful.

Oriental Fruit Moth, Grapholitha molesta (Busck).—The parasite *Macrocentrus ancylivorus* Roh. was introduced from New Jersey, U.S.A., in 1929 and 1930, when the "peach moth," as it was then known, threatened to wipe out the peach growing industry which had made the Niagara district of Ontario famous. Colonies of the parasite became established at once, and, supported by continued releases of laboratory-propagated individuals during the next 5 years, *M. ancylivorus* spread over the entire area and became the most important biotic factor in control of the moth.

Satin Moth, Stilpnotia salicis (L.).—Throughout the Maritime Provinces and Quebec, as in the New England States, the satin moth has been held in check for more than 25 years by 3 European species of parasites. *Apanteles solitarius* (Ratz.) was introduced as a specific parasite of the satin moth and, having several generations annually, it is very effective in reducing incipient outbreaks. *Meteorus versicolor* (Wesm.) and *Compsilura concinnata* (Mg.), which were established as parasites of the brown-tail moth, are very effective parasites of the satin moth as well. All 3 species were colonized in British Columbia between 1929 and 1934 by transfer of stock from the east, and as a result of their effectiveness no widespread outbreak of the satin moth has occurred there since 1934. Larvae collected from occasional lightly infested trees during the last 3 years have shown all 3 parasites present and their action in keeping the population at a low level is greatly retarding its spread to the Prairie Provinces.

European Spruce Sawfly, Diprion hercyniae (Htg.).—The introduction of parasites for control of this pest was begun in 1932 and represents the most ambitious and exhaustive effort in biological control yet attempted in Canada. With the larch sawfly scourge still fresh in the memory of many, the threat of similar devastation of the spruce forests prompted the bringing in of natural enemies of any and all species of sawflies found in Europe, or elsewhere, on the chance that they might, when released, attack this new pest. The insect was at first incorrectly named *Diprion polytenum* Htg., a European species similar in many respects to but differing biologically from the Canadian pest. Fortunately, natural enemies of both species were obtained, along with those of numerous species of pine sawflies, and among the 31 species of parasites released were 2 larval parasites, *Drino bohemica* Mesn. and *Exenterus vellicatus* Cush., which appear to be specific parasites of *D. hercyniae*. Several species of parasites became temporarily established in the extremely heavy and widespread population present between 1933 and 1940. The cocoon parasite *Dahlbominus fuscipennis* (Zett.), of which more than 850 million individuals were released, played an important part in reducing the enormous stock of larvae that accumulated in diapause in cocoons in the heavily infested areas. It is believed also that this parasite was responsible for introduction of the virus disease that brought about the rapid decline of the outbreak. The parasites *D. bohemica* and *E. vellicatus* appear to have become permanently established and are now important factors in keeping the sawfly population at a low level.

Others.—To the foregoing may be added numerous other successes: The oystershell scale, *Lepidosaphes ulmi* (L.), was reduced to a minor pest in British Columbia by the introduction of the predacious mite *Hemisarcoptes malus* (Shimer) from New Brunswick in 1917; the apple mealybug, *Phenacoccus aceris* (Sign.), has been controlled in the Kootenay Valley and on Vancouver Island, British Columbia, by the parasite *Allotropa utilis* Mues., introduced from Nova Scotia between 1938 and 1945; the hazel-nut scale, *Eulecanium coryli* (L.), at one time considered one of the most serious pests on the west coast, has not been of economic importance for the past 20 years because of parasitism by the chalcid *Blastothrix sericea* (Dalm.), introduced from England in 1928 and 1929.

The European wheat stem sawfly, *Cephus pygmaeus* (L.), was brought under control in Ontario by the introduction from England of 2 parasites, *Collyria calcitrator* (Grav.) and *Pleurotropis benefica* Gahan; in the last few years the sawfly has been exceedingly scarce and nearly all of the larvae collected have contained the parasite *C. calcitrator.* The pea moth, *Laspeyresia nigricana* (Steph.), was reduced from a serious pest to one of minor importance in British Columbia by the parasites *Ascogaster quadridentata* Wesm. and *Glypta haesitator* Grav., introduced from England between 1937 and 1939. Local outbreaks of several species of pine sawflies have been controlled by mass releases of the cocoon parasites *D. fuscipennis* and *Monodontomerus dentipes* (Dalm.). The apple woolly aphid, *Eriosoma lanigerum* (Hausm.), was controlled in British Columbia for more than 10 years after colonization of the parasite *Aphelinus mali* (Hald.), introduced from Ontario. As for many beneficial species in orchards, the activities of this parasite were temporarily reduced by the widespread use of DDT for codling moth control, but there are indications that this is being overcome by the development of resistant strains and by adjustment of control practices. Control of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westw.), on susceptible greenhouse crops such as tomatoes and cucumbers, is accomplished by the parasite *Encarsia formosa* Gahan when the temperature is maintained at 65° or higher; this parasite is maintained at Belleville in sufficient quantity to provide for restocking of greenhouse on request of growers. Introduced parasites have also given important assistance in control of the holly leaf miner, *Phytomyza ilicis* Curt., the larch casebearer, *Coleophora laricella* (Hbn.), the European earwig, *Forficula auricularia* (L.), the Comstock mealybug, *Pseudococcus comstocki* (Kuw.), and greenhouse mealybugs, *Pseudococcus* spp.

None of the pests referred to in this section, except the oriental fruit moth, have been attacked in appreciable numbers by locally occurring parasites.

Use of Disease Organisms in Biological Control

The importance of disease organisms in relation to insect populations has long been recognized and numerous attempts have been made in Canada to develop their use in control of pests. The first success in this field was the technique developed for use of the fungous disease *Entomophthora sphaerosperma* Fres. by which the apple sucker, *Psylla mali* (Schmdb.), was practically exterminated from certain orchards in Nova Scotia during 1922 and 1923. With greatly improved equipment for the study of microorganisms, notable advances have been made in research on insect diseases. The rapid decline of the spruce sawfly outbreak due to a virus disease emphasized the possibilities of utilizing such organisms in pest control and led to the establishment by the Forest Biology Division of the Insect Pathology Laboratory at Sault Ste. Marie, Ontario, especially equipped and staffed to study virus and other organisms causing disease in forest insects. A virus disease of a pine sawfly *Neodiprion sertifer* (Geoff.), which was introduced from England, has been cultured and used effectively during the past 2 years against this pest in Ontario and in New Jersey, U.S.A.

At the Kingston laboratory, bacterial and fungous diseases of grasshoppers and the codling moth are being investigated, and special attention is given to methods of mass culture and distribution. Diseases of mosquitoes and black flies caused by nematodes and protozoa are being studied at the Belleville laboratory.

Biological Control of Weeds

The biological control of weeds was undertaken for the first time in Canada with the introduction in 1951 of the chrysomelid beetles *Chrysolina hyperici* (Forst.) and *Chrysolina gemellata* Rossi for control of the common St. John's-wort, *Hypericum perforatum* L., in British Columbia. This step was taken following the control of the weed in California by these beetles of European origin introduced from Australia. Stock of the beetles was obtained by collection in California, Oregon, and Idaho, and 3 colonies were released during 1951 and 1952 in the Kootenay and Okanagan valleys. Establishment of both species at all points of release was confirmed in 1953 and the results are being followed in a series of carefully laid-out plots.

The possibilities of employing biological agents in the control of other noxious weeds are being investigated, special attention being directed toward control of Canada thistle, *Cirsium arvense* (L.) Scop., and toadflax, *Limaria vulgaris* Hill. Experiments in biological control of gorse, *Ulex europaeus* L., and Scotch broom, *Cytisus scoparius* (L.) Link, now being carried out in the United States, are also being watched with interest as some measure of control of these pests on the west coast appears desirable.

Present Activities and Trends

The results of 40 years of work have clearly shown the value of the biological method of controlling pests in Canada. Although made much more complex in its application by the annually increasing use of chemicals, those engaged in carrying out control by chemical and cultural methods are recognizing the necessity for harmonizing these with the requirements of biological agents with a view to developing more lasting control when emerging relief has been provided.

The differential effects of chemicals on beneficial and noxious species may be turned to our advantage by the development of tolerant or resistant strains of the beneficial species. Basic research in this and related fields is being carried out at Belleville and some success has been achieved in building up a strain of the parasite *Macrocentrus ancylivorus* Roh. with high tolerance to DDT. An important prerequisite in any biological control project is a complete knowledge of the organism to be used and its mode of action, together with the ability to produce it at will in any number required. Field observations and investigations are, therefore, being supplemented by basic research in such fields as insect nutrition, physiology, genetics, population ecology, host selectivity, and physical requirements. Research in nutrition and physiology has made possible the development of synthetic media in which certain species of insects can be grown. One dipterous parasite has been grown aseptically from egg to adult on a chemically defined synthetic diet. The application of results of such fundamental research should do much to further the practice of biological control in the future. A number of practical projects in course of development have already been referred to and others of major importance concern the spruce budworm, *Choristoneura fumiferana* (Clem.), the balsam woolly aphid, *Adelges piceae* (Ratz.), and complex groups of root maggots and orchard mites. These and many others present a challenge to our best efforts in biological control.

AN ANNOTATED LIST OF INFECTIOUS DISEASES OF INSECTS IN HAWAII[1]

By YOSHINORI TANADA
Agricultural Experiment Station
College of Agriculture, University of Hawaii
Honolulu, Hawaii

Infectious diseases of insects in Hawaii are not as well known as the other biological control agents and a summary of available information on them should be of value. Although many diseases of Hawaiian insects have been reported, the number of specifically identified pathogens is relatively few. Because of the large number of unidentified diseases, this list has been compiled under two tables. The first table contains the infectious microorganisms which have been identified as to genus or species, and the second contains those which have been recorded under a general name.

There are undoubtedly some misidentifications especially of the pathogens, but without actual specimens, these cannot be corrected. Repetitions, especially in Table II, where the specific names of the pathogens are unknown, are perhaps present.

In Hawaii, there appears to be only one identified species of bacteria recorded from insects found in the field (Table I). This is the American foulbrood of honeybee, which was first reported in 1931 by Fullaway. In Table II, there are two other unidentified bacterial diseases which were reported from *Anomala orientalis* Waterhouse (see Muir 1912a, b; Williams 1931) and from *Pieris rapae* (Linn.) (see Fullaway and Krauss 1945). The disease in *P. rapae* is probably caused by a granulosis virus (Tanada 1953b). Under laboratory conditions, the milky disease bacteria and *Bacillus thuringiensis* Berliner were found infectious to Hawaiian insects (Carter 1941; Tanada unpublished record).

The majority of insect diseases reported from Hawaii are caused by fungi. Most of the fungous diseases are found on scales, mealybugs, leaf hoppers and beetles. Some of these diseases are very effective in reducing the population of certain insect species. The entomogenous fungi, according to Williams (1931), probably destroy more mealybugs in the tropics than do all predators and insect parasites combined. Swezey (1936b) stated that almost the entire population of sugar cane leaf hopper, *Perkinsiella saccharicida* Kirkaldy, is sometimes destroyed by one or more fungi in the regions of greatest humidity. The green muscardine, *Metarrhizium anisopliae* (Metsch.), is reported to be effective against the Chinese rose beetle, *Adoretus sinicus* Burmeister, during wet seasons (Kotinsky 1905; Ehrhorn 1916; Swezey 1917, 1936a). The white halo fungus, *Verticillium lecanii* (Zimmerman), is very effective in controlling the green scale, *Coccus viridis* (Green), on coffee in Kona, Hawaii during the wet seasons.

---

[1] Published with the approval of the Director of the Hawaii Agricultural Experiment Station as Miscellaneous Paper No. 56.

There is some question as to the identity of some of the fungi given in Table I. Beardsley (1952) has pointed out that the fungous disease of green scale, *Coccus viridis*, reported by Ehrhorn (1931) and Zimmerman (1948e) is probably caused by *Verticillium lecanii* rather than *Entomophthora pseudococci* Speare. Other species that are in doubt are so indicated by question marks.

Only two virus diseases of insects have been specifically identified from Hawaii. One is the sacbrood of honeybee (Keck 1937; Eckert and Bess 1952) and the other is a granulosis of the imported cabbage worm, *Pieris rapae* (Linn.) (see Holdaway and Lucas 1941; Tanada 1953b). Several other cases have been designated as virus in nature because the insects died in a wilted condition, but without more detailed information the identity of the disease is still unknown.

All five of the protozoan infections which have been identified are caused by Microsporidia. A sixth unspecified infection in termites was reported by Silvestri (1909). The microsporidian, *Perezia mesnili* Paillot, has been found parasitizing over 50 per cent of the imported cabbage worms, *P. rapae*, in certain areas of Hawaii (Tanada unpublished record). The adult butterflies transmit this microsporidian to their offspring through the eggs.

Several insects are attacked by nematodes belonging to the genera *Gordius* and *Rhabditis*, while others are attacked by unspecified nematodes (Table II). Since the association of nematodes with insects may range from non-parasitism to obligate parasitism (Steinhaus 1949), some of the nematodes reported above may be saprophytes rather than parasites.

Applied Insect Pathology in Hawaii

Applied insect pathology, a branch of biological control of insect pests, has had only limited applications in Hawaii. Relatively few infectious microorganisms have been introduced as compared to the number of insect parasites and predators, and many of the microorganisms became established without intentional introduction by man.

The report of Koebele (1897) appears to be one of the earliest record of an introduction of infectious microorganisms into Hawaii. He reported that two species of fungi which parasitized Coccidae (=Lecanidae) had become established and spread over most parts of the islands. He did not identify the fungi to species. In 1901a, he received from Hong Kong a fungus attacking *Pulvinaria psidii* Mask. Perkins, in 1906, introduced a fungus on leaf hoppers from Australia. The fungus, *Sphaerostilbe coccophila* Tul., from Florida has become established according to Kotinsky (1906). A fungus on whitefly was introduced by Kotinsky (1909) from Florida. Speare (1912) received *Sterigmatocystis ferruginea* from Japan for the control of *Adoretus sinicus* but apparently the fungus was not pathogenic to the beetle. A fungus which was obtained from Japan on *Mimela flavilabris* (Waterhouse) (=*Anomala flavilabris* Waterhouse) was apparently the same as that introduced by Muir from the Philippines (Ehrhorn 1920). In 1929, Illingworth reported that a fungus attacking the green scale, *Coccus viridis*, was introduced from Florida and became very effective in controlling the green scale on coffee. This may be the white halo fungus, *Verticillium lecanii.*

According to Van Zwaluwenburg (1927) and Pemberton (1928), the nematodes (*Rhabditis* spp.) from Celebes and North Borneo could not be reared on termites in Hawaii. In 1928, Van Zwaluwenburg reported that an abdominal nematode (*Termes* sp.) from Celebes could not be transmitted to *Coptotermes formosanus* Shiraki. Head infecting nematodes from Borneo also gave negative results (Van Zwaluwenburg 1928; Pemberton 1928).

Fullaway (1941, 1943) introduced the nematode and bacillus which are highly infectious to the Japanese beetle, *Popillia japonica* Newm., but no conclusion was reached on their effectiveness against the scarab beetles in Hawaii. The bacterium, probably *Bacillus popilliae* Dutky, causing milky disease of the Japanese beetle, was found effective against both the Chinese rose beetle, *Adoretus sinicus*, and the anomala beetle, *Anomala orientalis*, under laboratory conditions (Carter 1941).

The fungus, *Beauveria bassiana* (Balsamo), was introduced by the Hawaii Board of Agriculture and Forestry (1952) from Louisiana to control the sweet potato weevil, *Cylas formicarius elegantulus* (Summers), and the West Indian sweet potato weevil, *Euscepes postfasciatus* (Fairmaire). However this fungus was apparently present in Hawaii before the above introduction (Sherman 1952). Spores of *Bacillus thuringiensis* were obtained in 1952 from Dr. E. A. Steinhaus in California, and were tested against *Pieris rapae* in the field (Tanada unpublished record).

In Hawaii, there have been very few attempts to utilize infectious microorganisms in the field for the control of insect pests. Koebele, in 1897, reported that a greenish grey fungus of Chinese rose beetle, *Adoretus sinicus* (misidentified as *A. umbrosus* var. *tenuimaculatus)* was disseminated in Hawaii by distributing diseased beetles. This fungus is probably the green muscardine, *Metarrhizium anisopliae.* During the period from 1901 to 1915, the Hawaii Board of Agriculture and Forestry carried out an extensive program of distributing Chinese rose beetles, which had been inoculated with the green muscardine, throughout the Hawaiian Islands wherever the beetles were present in large numbers. The following men, A. Craw, E. M. Ehrhorn, G. W. Kirkaldy, A. Koebele, J. Kotinsky and B. M. Newell, were involved in the propagation and distribution of the fungus. The fungus apparently reduced the Chinese rose beetle population especially during rainy months and in regions where the fungus was previously absent or scarce. Van Dine (1904) reported that efforts to disseminate a fungus, *Isaria* sp., in the cane field against the sugar cane leaf hopper was unsuccessful.

In 1948, Pemberton attempted to control the army worm, *Laphygma exempta* (Walker), with a wilt disease which was apparently caused by a virus, but his attempt was not successful. However, this disease is often very effective under natural conditions as pointed out by Williams (1931), who stated, ". . . when the climatic conditions favor the disease it is perhaps more effective than all the predators and other parasites combined."

In 1952, the Department of Entomology of the Hawaii Agricultural Experiment Station established a project, "The Infectious Diseases of Insects in Hawaii and the Use of Microorganisms for the Control of Insect Pests." At present, studies are being conducted on the use of infectious diseases for the control of insects on cabbage.

LITERATURE CITED

BEARDSLEY, J. W. 1952. A fungus parasite of *Coccus viridis* (Green) in Hawaii. Master's thesis. 59 pp. University of Hawaii, Honolulu.

————. 1953. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 15: 10.

BRIDWELL, J. C. 1920. Miscellaneous notes by Mr. Bridwell. *Proc. Haw. Ent. Soc.* 4: 328-329.

CARTER, W. 1941. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 11: 14-16.

CHAMBERLAIN, J. E. 1882. The Peelua or armyworm of the Hawaiian Islands. Thrum's Haw. Almanac 1883: 44-50.

CHOCK, Q. C. 1932. Report of assistant entomologist, July, 1932. *Haw. Forester & Agr.* 29: 121.

Craw, A. 1906. Leaf hoppers and their natural enemies. *Haw. Planters' Monthly.* 25: 136-152.

Eckert, J. E. 1951. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 14: 222-224.

——— and H. A. **Bess.** 1952. Fundamentals of beekeeping in Hawaii. *Univ. Haw. Ext. Bul.* 55: 59 pp.

Ehrhorn, E. M. 1910. Division of entomology. *Haw. Forester & Agr.* 7: 140-141, 176-177.

———. 1916. Inspection of nursery stock and control of insect pests and plant diseases. *Haw. Forester & Agr.* 13: 160-163.

———. 1920. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 4: 438-439.

———. 1923. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 5: 204.

———. 1931. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 7: 369-372.

Fullaway, D. T. 1920. Natural control of scale insects in Hawaii. *Proc. Haw. Ent. Soc.* 4: 237-246.

———. 1921. The fern weevil. (*Syagrius fulvitarsis* Pasc.). *Haw. Forester & Agr.* 18: 101-114.

———. 1931. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 7: 335-338.

———. 1932. Division of Entomology. *Haw. Forester & Agr.* 29: 97-98.

———. 1933. Division of Entomology. *Haw. Forester & Agr.* 30: 55-58.

———. 1941. Report of the territorial entomologist and chief plant inspector. *Haw. Board Commissioners Agr. & For. Bien. Rpt.* 1938-40. pp. 19-22.

———. 1943. Division of Entomology. Report of the territorial entomologist and chief plant inspector. *Haw. Board Commissioners Agr. & For. Bien. Rpt.* 1940-42. pp. 28-32.

——— and N. L. H. **Krauss.** 1945. Common insects of Hawaii. 228 pp. Tongg Publishing Co., Honolulu.

Hadden, F. C. 1928. Sugar cane mosaic and insects. *Haw. Planters' Record.* 32: 130-142.

Hagen, K. S. 1952. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 14: 344-347.

Hawaii Board of Agriculture and Forestry. 1901. Government entomologist. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1900. pp. 17-18.

———. 1903. Blights and insect pests. *Haw. Board Commissioners Agr. & For. Bien. Rpt.* 1900-02. pp. 36-38.

———. 1950. Division of Entomology. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1950. pp. 20-27.

———. 1952. Division of Entomology and Marketing. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1952. pp. 27-58.

Hebard, M. 1922. Dermaptera and Orthoptera of Hawaii. *B.P. Bishop Mus. Occ. Papers.* 7: 305-387.

Holdaway, F. G. and E. **Lucas.** 1941. Biological control of cabbage worm. *Haw. Agr. Exp. Sta. Rpt.* 1940. pp. 41-42.

Illingworth, J. F. 1917. Entomological program. *Proc. Haw. Ent. Soc.* 3: 275.

———. 1929. Preliminary notes on pests of agricultural crops of Kona, March 15, 1928. *Proc. Haw. Ent. Soc.* 7: 248-254.

ILLINGWORTH, J. F. 1932. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 8: 22-25.

KECK, C. B. 1937. Presidential address: observations on beekeeping in Hawaii. *Proc. Haw. Ent. Soc.* 9: 461-467.

KIRKALDY, G. W. 1904. A preliminary list of the insects of economic importance recorded from the Hawaiian Islands. *Haw. Forester & Agr.* 1: 183-189.

————. 1905. Report of G. W. Kirkaldy, acting superintendent of entomology. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1904. pp. 122-136.

KOEBELE, A. 1897. Report of the entomologist of the Hawaiian government. *Haw. Planters' Monthly.* 16: 67-85.

————. 1901a. (Report No. 3) Report of Professor Albert Koebele, entomologist. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1900. pp. 36-49.

————. 1901b. (Report No. 4) Report of Prof. Koebele on destruction of forest trees, Hawaii. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1900. pp. 50-60.

KOTINSKY, J. 1905. The Japanese beetle fungus. *Haw. Forester & Agr.* 2: 361-363.

————. 1906. Report of the assistant entomologist. *Haw. Boarl Commissioners Agr. & For. Ann. Rpt.* 1905. pp. 113-144.

————. 1909. Report of superintendent of entomology for June, 1909. *Haw. Forester & Agr.* 6: 337-339.

LARSEN, L. D. 1911a. A fungus parasite of the cane mealy bug. *Haw. Planters' Record.* 4: 249-252.

————. 1911b. Fighting the cane froghopper in Trinidad by means of a fungus parasite. *Haw. Planters' Record.* 5: 3-5.

LOOK, W. C. 1941. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 11: 7-9.

————. 1943. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 11: 269-271.

MARSH, H. O. 1911. Some experiments on the chrysanthemum plant louse. (*Macrosiphum sanborni* Gillette). *Haw. Board Commissioners Agr. & For. Bien. Rpt.* 1908-10. pp. 160-172.

MUIR, F. 1912a. The Anomala root-grub. *Haw. Planters' Record.* 7: 53.

————. 1912b. Report on the Anomala root-grub. *Haw. Planters' Record.* 7: 226-232.

————. 1921. The sugar cane leaf hopper and its parasites in Hawaii. *Haw. Planters' Record.* 25: 108-123.

———— and O. H. SWEZEY. 1916. The cane borer beetle in Hawaii and its control by natural enemies. *Haw. Sugar Planters' Assoc. Ent. Series. Bul.* No. 13. 103 pp.

NAKAO, H. 1953. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 15: 7.

PEMBERTON, C. E. 1927. Reports on foreign work in entomology. *Haw. Planters' Record.* 31: 21-25.

————. 1928. Nematodes associated with termites in Hawaii, Borneo and Celebes. *Proc. Haw. Ent. Soc.* 7:148-150.

————. 1948. The control of the grass armyworm, *Laphygma exempta* (Walker), in Hawaii by parasites. *Haw. Planters' Record.* 52: 181-200.

PEMBERTON, C. E. and F. X. WILLIAMS. 1938. Some insect and other animal pests in Hawaii not under satisfactory biological control. *Haw. Planters' Record.* 42: 211-230.

PERKINS, R. C. L. 1903. The leaf hopper of the sugar cane. *Haw. Board Commissioners Agr. & For. Div. Ent. Bul.* No. 1. 38 pp.

———. 1906. Leaf hoppers and their natural enemies (introduction). *Haw. Sugar Planters' Assoc. Ent. Series Bul.* No. 1. 32 pp.

———. 1913a. Review of the Coleoptera. In: Introduction to Fauna Hawaiiensis. David Sharp, Ed. cxii-cxliv. Cambridge Univ. Press, London.

———. 1913b. Review of the Lepidoptera. In: Introduction to Fauna Hawaiiensis. David Sharp, Ed. cxliv-clxx. Cambridge Univ. Press, London.

———. 1913c. Review of the Hemiptera. In: Introduction to Fauna Hawaiiensis. David Sharp, Ed. cxc-ccxi. Cambridge Univ. Press, London.

———. 1913d. Review of the Orthoptera. In: Introduction to Fauna Hawaiiensis. David Sharp, Ed. ccxi-ccxx. Cambridge Univ. Press, London.

SAKIMURA, K. 1937. On the bionomics of *Thripoctenus brui Vuillet,* a parasite of *Thrips tabaci* Lind., in Japan. *Kontyû.* 11: 370-390, 410-424.

SHERMAN, M. 1952. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 14: 353-356.

SILVESTRI, F. 1909. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 2: 36-37.

SPEARE, A. T. 1912a. Fungi parasitic upon insects injurious to sugar cane. *Haw. Sugar Planters' Assoc. Path. Physiol. Series Bul.* No. 12. 62 pp.

———. 1912b. A fungus disease of the borer beetle. *Haw. Planters' Record.* 6: 121-126.

STEINHAUS, E. A. 1949. Principles of insect pathology. 757 pp. McGraw-Hill Book Co., Inc., New York.

SWEZEY, O. H. 1913. Sugar cane mealy bugs in the Hawaiian Islands. *Haw. Planters' Record.* 8:200-208.

———. 1917. Insect pests of truck crops. *Haw. Planters' Record.* 16: 426-435.

———. 1926. Reports on defoliation of Maui koa forests by caterpillars. *Haw. Planters' Record.* 30: 354-362.

———. 1927. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 6: 346-347.

———. 1929. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 7: 202-203.

———. 1936a. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 9: 129-133.

———. 1936b. Biological control of the sugar cane leaf hopper in Hawaii. *Haw. Sugar Planters' Assoc. Ent. Series Bul.* No. 21. 101 pp.

SWEZEY, O. H. and E. H. BRYAN. 1929. Further notes on the forest insects of Molokai. *Proc. Haw. Ent. Soc.* 7: 293-314.

TANADA, Y. 1951. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 14: 208-210.

———. 1953a. A microsporidian parasite of the imported cabbage worm in Hawaii. *Proc. Haw. Ent. Soc.* 15: 167-175.

———. 1953b. Description and characteristics of a granulosis virus of the imported cabbage worm. *Proc. Haw. Ent. Soc.* 15: 235-260.

TERRY, F. W. 1907. The sugar cane borer (*Sphenophorus obscurus*) in the Hawaiian Islands. *Haw. Sugar Planters' Assoc. Div. Ent. Cir.* No. 3. 22 pp.

THOMSEN, W. 1951. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 14: 205-207.

VAN DINE, D. L. 1904. A sugar cane leaf hopper in Hawaii. *Haw. Agr. Exp. Sta. Bul.* No. 5. 29 pp.

VAN ZWALUWENBURG, R. H. 1927. Nematode parasites of termites. *Haw. Planters' Record.* 31: 209-210.

————. 1928. The interrelationships of insects and roundworms. *Haw. Sugar Planters' Assoc. Ent. Series Bul.* No. 20. 68 pp.

WEBER, P. W. 1951. Notes and exhibitions. *Proc. Haw. Ent. Soc.* 14: 208-210.

WILLIAMS, F. X. 1928. The Kamehameha Butterfly, *Vanessa tammeamea* Esch. *Proc. Haw. Ent. Soc.* 7:164-169.

————. 1931. The insects and other invertebrates of Hawaiian sugar cane fields. 400 pp. *Haw. Sugar Planters' Assoc. Exp. Sta.*, Honolulu.

ZIMMERMAN, E. C. 1948a. Insects of Hawaii. vol. 1, 206 pp. Univ. Hawaii Press, Honolulu.

————. 1948b. Insects of Hawaii. vol. 2, 475 pp. Univ. Hawaii Press, Honolulu.

————. 1948c. Insects of Hawaii. vol. 3, 255 pp. Univ. Hawaii Press, Honolulu.

————. 1948d. Insects of Hawaii. vol. 4, 268 pp. Univ. Hawaii Press, Honolulu.

————. 1948e. Insects of Hawaii. vol. 5, 464 pp. Univ. Hawaii Press, Honolulu.

Literature on the Propagation and Distribution of Metarrhizium anisopliae.

CRAW, A. 1907. Division of Entomology. Report of Superintendent of entomology and inspector. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1906. pp. 139-158.

EHRHORN, E. M. 1911. Division of Entomology. Report of the superintendent of entomology for 1909. *Haw. Board Commissioners Agr. & For. Bien. Rpt.* 1908-10. pp. 103-123.

————. 1911. Report of superintendent of entomology for 1910. *Haw. Board Commissioners Agr. & For. Bien. Rpt.* 1908-10. pp. 125-151.

————. 1911, 1912, 1913, 1914, 1915. Division of Entomology. *Haw. Forester & Agr.* 8: 51-53, 123-125, 218-219, 236-237, 296-298; 9: 122-123, 290-291, 315-317; 10: 131-132, 151-153, 263-268, 341-343; 11: 10-12, 193-195, 264-266; 12: 177-179, 278-281, 333-336.

Hawaii Board of Agriculture and Forestry. 1901. Government entomologist. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1900. pp. 17-18.

————. 1903. Blights and insect pests. *Haw. Board Commissioners Agr. & For. Bien. Rpt.* 1900-02. pp. 36-38.

KIRKALDY, G. W. 1905. Report of G. W. Kirkaldy, acting superintendent of entomology. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1904. pp. 122-136.

KOEBELE, A. 1897. Report of the entomologist of the Hawaiian government. *Haw. Planters' Monthly.* 16: 67-85.

KOEBELE, A. 1901. (Report No. 3) Report of Professor Albert Koebele, entomologist. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1900. pp. 36-49.

KOTINSKY, J. 1905. The Japanese beetle fungus. *Haw. Forester & Agr.* 2: 361-363.

————. 1905, 1906. Report of the assistant entomologist. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1904. pp. 147-159; 1905. pp. 113-144.

————. 1908. Introduction, breeding and distribution of beneficial insects. *Haw. Board Commissioners Agr. & For. Ann. Rpt.* 1907. pp. 85-89.

————. 1909. Division of Entomology. Report of superintendent of entomology for September. *Haw. Forester & Agr.* 6: 434-437.

NEWELL, B. M. 1905. How to inoculate Japanese beetles. (*Adoretus umbrosus*, var. *tenuimaculatus.*) *Haw. Forester & Agr.* 2: 363-364.

MARSH, H. O. 1910. Rept. Div. Ent. 1910. Bd. Agr. and For., Hawaii: 152-159.

MCPHAIL, M. 1943. Linsed oil soap—a new lure for melon fly. *Jour. Econ. Ent.* 36: 426-29.

NISHIDA, T. and H. A. BESS. 1950. Applied ecology in melon fly control. *Jour. Econ. Ent.* 43: 877-83.

SEVERIN, H. H. P., H. C. SEVERIN, and W. J. HARTUNG. 1914. The ravages, life history, weights of stages, natural enemies and methods of control of the melon fly (*Dacus cucurbitae* Coq.). *Ann. Ent. Soc. Amer.* 7(3): 177-207.

STEINER, L. F. and F. G. HINMAN. 1952. Field tests of insecticides for control of oriental fruit fly. *Jour. Econ. Ent.* 45(3): 388-395.

VAN DEN BOSCH, ROBERT, H. A. BESS, and F. H. HARAMOTO. 1951. Status of oriental fruit fly parasites in Hawaii. *Jour. Econ. Ent.* 44(5): 753-759.

TABLE I

INFECTIOUS INSECT DISEASES IN HAWAII WHOSE PATHOGENS HAVE BEEN IDENTIFIED TO GENERA OR SPECIES.

TYPE OF INFECTION	PATHOGEN	HOST	LABORATORY OR FIELD INFECTION	REFERENCES
Bacterial	*Bacillus larvae* White	*Apis mellifera* Linn.	Field	Fullaway 1931, 1932; Chock 1932; Fullaway 1933; Keck 1937; Fullaway & Krauss 1945; Eckert 1951; Thomsen 1951; Eckert & Bess 1952.
Bacterial	Milky disease bacteria (prob. *Bacillus popilliae* Dutky)	*Adoretus sinicus* Burmeister (*Adoretus umbrosus***)	Laboratory	Carter 1941.
		Anomala orientalis Waterhouse	Laboratory	Carter 1941.
Bacterial	*Bacillus thuringiensis* Berliner	*Pieris rapae* (Linn.)	Laboratory	Tanada*.
		Plutella maculipennis (Curt.)	Laboratory	Tanada*.
Fungous	*Myiophagus* sp. (prob. *ucranicus* [Wize])	*Lepidosaphes beckii* (Newman)	Field	Hawaii Board Agr. & For. 1950; Weber 1951.
Fungous	*Entomophthora pseudococci* Speare	*Ferrisiana virgata* (Cockerell) (=*Pseudococcus virgatus* (Cockerell))	Laboratory	Speare 1912a.
		Saccharicoccus sacchari (Cockerell) (=*Trionymus sacchari* (Cockerell), *Pseudococcus sacchari*,	Field	Speare 1912a; Swezey 1913; Fullaway 1920; Ehrhorn 1931; Zimmerman 1948e.

---

* Unpublished record.

** Misidentification in Hawaiian records.

TABLE I (continued)

Type of Infection	Pathogen	Host	Laboratory or Field Infection	References
		*P. calceolariae***)		
		Dysmicoccus boninsis (Kuwana) (=*Pseudococcus boninsis* (Kuwana), *P. saccharifolii* (Green)**)	Field	Swezey 1913; Williams 1931.
		Dysmicoccus brevipes Cockerell (=*Pseudococcus brevipes* (Cockerell), *P. bromeliae* (Bouche)**)	Field	Swezey 1913.
Fungous	*Entomophthora pseudococci* Speare?	*Coccus elongatus* (Signoret) (*Coccus longulus* (Doug.)**)	Field	Ehrhorn 1931; Zimmerman 1948e.
		Coccus viridis (Green)	Field	Ehrhorn 1931; Zimmerman 1948e.
		Saissetia nigra (Nietner)	Field	Ehrhorn 1931; Zimmerman 1948e.
Fungous	*Entomophthora sphaerosperma* Fresenius	*Pycnoderes quadrimaculatus* Guérin-Méneville	Field	Look 1941, 1943; Zimmerman 1948c.
Fungous	*Entomophthora* sp.	*Perkinsiella saccharicida* Kirkaldy	Field	Speare 1912a; Muir 1921; Williams 1931; Swezey 1936b; Zimmerman 1948d.
Fungous	*Sphaerostilbe coccophila* Tul.	*Lepidosaphes beckii* (Newman)	Field	Kotinsky 1906.
Fungous	*Cordyceps* sp. (prob. *Isaria Saussurei* Cooke =*Cordyceps sphecocephala*)	*Siphanta acuta* (Walker)	Field	Speare 1912a.
		Polistes sp.	Field	Speare 1912a.

** Misidentification in Hawaiian records.

TABLE I (continued)

Type of Infection	Pathogen	Host	Laboratory or Field Infection	References
Fungous	*Cordyceps* sp.	*Perkinsiella saccharicida* Kirkaldy	Field	Speare 1912a; Muir 1921; Williams 1931; Swezey 1936b; Zimmerman 1948d.
Fungous	*Aspergillus parasiticus* Speare	*Saccharicoccus sacchari* (Cockerell)	Field	Speare 1912a; Swezey 1913; Fullaway 1920; Williams 1931; Zimmerman 1948e.
		Dysmicoccus boninsis (Kuwana)	Field	Swezey 1913.
		Dysmicoccus brevipes (Cockerell)	Field	Swezey 1913.
Fungous	*Aspergillus* sp.	*Saccharicoccus sacchari* (Cockerell)	Field	Larsen 1911a.
Fungous	*Penicillium* sp. (prob. *Metarrhizium anisopliae* (Metsch.))	*Rhabdoscelus obscurus* (Boisd.) (=*Rhabdocnemis obscura* (Boisd.))	Field	Terry 1907.
Fungous	*Verticillium lecanii* (Zimmerman)	*Coccus viridis* (Green)	Field	Beardsley 1952, 1953.
		Ceroplastes rubens Maskell	Field	Beardsley 1952, 1953.
		Coccus acuminatus (Signoret)	Field	Beardsley 1952, 1953.
		Eucalymnatus tessellatus (Signoret)	Field	Beardsley 1952, 1953.
		Saissetia oleae (Bernard)	Field	Beardsley 1952, 1953.
Fungous	*Beauveria bassiana* (Balsamo)	*Cylas formicarius elegantulus* (Summers)	Laboratory	Hawaii Board Agr. & For. 1952; Nakao 1953.

TABLE I (continued)

Type of Infection	Pathogen	Host	Laboratory or Field Infection	References
		Euscepes postfasciatus (Fairmaire)	Laboratory	Hawaii Board Agr. & For. 1952.
Fungous	*Beauveria* sp.	*Cactoblastis cactorum* (Berg)	Field	Nakao 1953.
Fungous	*Beauveria* sp.	*Cylas formicarius elegantulus* (Summers)	Laboratory	Sherman 1952.
		Euscepes postfasciatus (Fairmaire)	Laboratory	Sherman 1952.
Fungous	*Sporotrichum* sp.? (=*Beauveria* sp.)	*Perkinsiella saccharicida* Kirkaldy	Field	Muir 1921; Williams 1931; Swezey 1936b; Zimmerman 1948d.
Fungous	*Sporotrichum* sp.? (=*Beauveria* sp.)	*Rhabdoscelus obscurus* (Boisd.)	Field	Williams 1931.
Fungous	*Isaria* sp.	*Siphanta acuta* (Walker)	Field	Van Dine 1904.
		Perkinsiella saccahricida Kirkaldy	Field	Van Dine 1904.
Fungous	*Metarrhizium anisopliae* (Metsch.)	*Laphygma exempta* (Walker) (*Spodoptera mauritia* [Boisd.]**)	Field	Williams 1931.
		Rhabdoscelus obscurus (Boisd.)	Field	Koebele 1897; Larsen 1911b; Speare 1912a, b; Muir & Swezey 1916; Williams 1931; Fullaway & Krauss, 1945.
		Adoretus sinicus Burmeister	Field	Koebele 1897; Hawaii Board Agr. & For. 1901, 1903; Larsen 1911b; Speare 1912a,b; Perkins 1913a; Muir & Swezey

---

** Misidentification in Hawaiian record.

TABLE I (continued)

Type of Infection	Pathogen	Host	Laboratory or Field Infection	References
				1916; Ehrhorn 1916; Swezey 1917; Williams 1931; Swezey 1936a; Fullaway & Krauss 1945.
		Anomala orientalis Waterhouse	Field	Speare 1912a; Muir 1912a,b; Williams 1931.
Fungous	*Acontium* sp.	*Macrosiphum sanborni* Gillette	Field	Marsh 1911.
Virus	*Morator aetatulae* Holmes	*Apis mellifera* Linn.	Field	Keck 1937; Eckert & Bess 1952.
Virus	*Bergoldia virulenta* Tanada	*Pieris rapae* (Linn.)	Field	Holdaway & Lucas 1941; Tanada 1953b.
Protozoan	*Nosema apis* Zander	*Apis mellifera* Linn.	Field	Eckert & Bess 1952.
Protozoan	*Nosema* sp.	*Dacus dorsalis* Hendel	Laboratory	Hagen 1952.
		Dacus cucurbitae Coquillett	Laboratory	Hagen 1952.
		Ceratitis capitata (Wied.)	Laboratory	Hagen 1952.
Protozoan	*Perezia mesnili* Paillot	*Pieris rapae* (Linn.)	Field	Tanada 1953a.
Nematode	*Gordius* sp.	*Polistes fuscatus* (F.) var. *aurifer* (Saussure)	Field	Swezey 1929.
Nematode	*Gordius* sp.	*Oxya chinensis* (Thunberg)	Field	Swezey 1927; Zimmerman 1948b.
Nematode	*Gordius* sp.	Gryllidae (endemic spp.)	Field	Perkins 1913d.
Nematode	*Gordius* sp.	*Paratrigonidium* Brunner	Field	Zimmerman 1948b.
Nematode	*Rhabditis* sp.	*Neotermes connexus* Snyder	Field?	Pemberton 1928.

TABLE II

INFECTIOUS INSECT DISEASES IN HAWAII WHOSE PATHOGENS HAVE NOT BEEN SPECIFICALLY IDENTIFIED

TYPE OF INFECTION	HOST	LABORATORY OR FIELD INFECTION	REFERENCES
Bacterial	*Anomala orientalis* Waterhouse	Field	Muir 1912a, b; Williams 1931.
Bacterial	*Pieris rapae* (Linn.)	Field	Fullaway & Krauss 1945.
Fungous	Blattidae	Field	Koebele 1897.
Fungous	*Coccus viridis* (Green)	Field	Illingworth 1929, 1932; Pemberton & Williams 1938; Fullaway & Krauss 1945.
Fungous	*Coccus elongatus* (Signoret) (*Lecanium longulum***)	Field	Koebele 1901b; Ehrhorn 1923.
Fungous	*Saissetia nigra* (Nietner) (=*Lecanium nigrum* Nietner)	Field	Koebele 1901b; Illingworth 1929.
Fungous	*Diaspis bromeliae* (Kerner)	Field	Kotinsky 1909.
Fungous	Coccidae (=Lecanidae)	Field	Koebele 1897, 1901a, b.
Fungous	*Aphis maidis* Fitch	Field	Hadden 1928; Zimmerman 1948e.
Fungous	*Siphanta acuta* (Walker)	Field	Kirkaldy 1904, 1905; Perkins 1913c; Zimmerman 1948d.
Fungous	*Perkinsiella saccharicida* Kirkaldy	Field & Laboratory	Perkins 1903; Kirkaldy 1905; Craw 1906; Perkins 1906.
Fungous	Delphacidae (endemic spp.)	Field	Perkins 1903, 1906; Craw 1906.
Fungous	*Nesophrosyne* spp.	Field	Perkins 1913c.
Fungous	Cicadellidae	Field	Zimmerman 1948a.
Fungous	Aleurodidae	Field	Zimmerman 1948e.
Fungous	*Scotorythra paludicola* (Butl.)	Field	Perkins 1913b; Swezey 1926.
Fungous	*Scotorythra idolias* Meyrick	Field	Koebele 1901b; Perkins 1918b.
Fungous	*Plusia chalcites* Esp.	Field	Perkins 1913b.
Fungous	Noctuidae	Field	Chamberlain 1882; Koebele 1897.
Fungous	Tineidae	Field	Koebele 1897.
Fungous	*Pieris rapae* (Linn.)	Field	Ehrhorn 1910; Tanada*.
Fungous	*Homoneura hawaiiensis* (Grimshaw)	Field	Tanada 1951.
Fungous	*Dacus dorsalis* Hendel	Field	Tanada 1951.
Fungous	*Eutreta xanthochaeta* Aldrich	Field	Tanada 1951.
Fungous	*Aegosoma reflexum* Karsch	Field	Koebele 1897.
Fungous	Nitidulidae	Field	Perkins 1913a.
Fungous	*Aphodius* sp.	Field	Koebele 1897.
Fungous	*Syagrius fulvitarsis* Pasc.	Field	Fullaway 1921.

* Unpublished record.
** Misidentification in Hawaiian records.

TABLE II (continued)

Type of Infection	Host	Laboratory or Field Infection	References
Virus	*Omiodes blackburni* (Butler)	Field	Illingworth 1917.
Virus	*Laphygma exempta* (Walker) (*Spodoptera mauritia***)	Field	Williams 1931; Pemberton 1948.
Virus	*Plusia* sp.	Field	Williams 1928.
Virus	*Vanessa tammeamea* Esch.	Field	Williams 1928.
Virus	*Scotorythra* sp.	Field	Williams 1928.
Protozoan	*Hellula undalis* (F.)	Laboratory	Tanada*.
Protozoan	Isoptera	Field	Silvestri 1909.
Nematode	*Coptotermes formosanus* Shiraki	Laboratory	Pemberton 1927 (note by Muir).
Nematode	*Thrips abdominalis* (Crawford)	Field	Sakimura 1937.
Nematode	*Prognathogryllus* sp.	Field	Van Zwaluwenburg 1928.
Nematode	*Oxya chinensis* (Thunberg)	Field	Van Zwaluwenburg 1928.
Nematode	*Paratrigonidium pacificum* Scudder	Field	Swezey & Bryan 1929.
Nematode	*Paratrigonidium varians* Perkins	Field	Hebard 1922.
Nematode	*Scotorythra* sp.	Field	Swezey 1927 (note by Fullaway).
Nematode	Lepidoptera	Field	Bridwell 1920.

* Unpublished record.
** Misidentification in Hawaiian records.

SOME FEATURES OF THE INSECT PESTS OF THE RICE PLANT IN HOKKAIDO, A NORTHERN LIMIT OF RICE CULTURE IN RELATION TO RECENT DEVELOPMENTS IN CULTURE METHODS

By Satoru Kuwayama
Hokkaido National Agricultural Experiment Station
Kotoni, Sapporo, Japan

Hokkaido is the northernmost of the four major islands of Japan. It lies approximately between 41°34′N and 45°31′N latitude and is bordered by the Sea of Japan, Sea of Okhotsk, and Pacific Ocean. Its climate is temperate, humid, and somewhat continental in character—fairly warm in the short summers but rather cold in the long winters. The frostless season ranges from 130 to 175 days. Nowadays, in this island, paddy fields occupy an approximate acreage of 135 thousand hectares, or 18 per cent of total cultivated land. They are distributed over the greater part of the island, where the mean temperature in the five months from May through September is over 15°C and that in the three months from June through August is over 17°C.

Historical Sketch of the Development of Rice Culture in Hokkaido

Though the beginning of rice culture in Hokkaido is said to date back to about 270 years ago, it had been considered up to the end of the Nineteenth Century that rice culture was unsuitable, because of the climate. Rice paddy fields were restricted only to a limited area in the south. It may be said that agriculture of Hokkaido practically got its start in 1869, after the establishment of a colonial office, called "Kaitakushi" which eventually became the Hokkaido Prefectural Office. At first the staff of the office made no attempt to promote rice culture. The immigrant farmers from southern Japan, however, persisted in their attempt to grow this crop, despite repeated failures. Then the research workers of our Experiment Station made continuous efforts to breed new varieties and to devise more adequate culture methods, as well as measures for control of rice pests and diseases. Success of the experiments on the method of direct sowing of rice seeds in 1893 and the development of seeding tools in 1905, as well as the promulgation of a special act regarding irrigation co-operatives in Hokkaido in 1902, gave impetus to the rice culture and led to remarkable expansion of paddy fields. Before that time rice had been mostly planted in paddy fields through use of nursery-grown rice transplants, similar to the practice in the southern regions of Japan. Moreover, breeders of our Experiment Station succeeded by hybridization in raising very precocious varieties which matured in approximately 110 or 120 days, such as "Hashiri-bozu" in 1924 and "Suito Norin No. 11" in 1937. The appearance of those new varieties stimulated a further expansion of paddy culture. The acreage in 1932 attained a maximum of 197 thousand hectares, or 23 per cent of the total acreage of cultivated land in Hokkaido. At that time, in nearly 83 per cent of the paddy fields, rice was planted by direct sowing of seeds, while in the remaining warmer areas of the island it was planted through use of nursery-grown rice transplants. In recent years, however, the acreage of paddy fields has been decreasing owing to a succession of bad harvests for several years during and after 1931 and also to war-time conditions. Since 1935 a method of culture by use of transplants grown in cold frames covered with some insulating materials, such as strips of oil-paper or in hotbeds, was developed and studied experimentally in an effort to reduce cold injuries. This method makes possible an earlier start of the seed and it makes seedlings available for transplanting early in the spring as soon as soil temperature of the paddy field permits. This method has been conducive to higher yields per unit of area, not only because of the increased certainty in harvest but also because of the possibility of using more prolific late-maturing varieties. Hence, this method has been rapidly becoming popular in Hokkaido during the past ten years. Below two tables on the changing aspects of rice culture in Hokkaido are given to facilitate comparison.

TABLE I

ACREAGE AND YIELDS PER UNIT OF AREA OF PADDY RICE IN HOKKAIDO

YEARS	AVERAGE ACREAGE		AVERAGE YIELDS PER HECTARE	
	HECTARES	RATIO	KILOLITRES	RATIO
1886–1895	2,390.0	100	2.129	100
1896–1905	11,841.4	495	1.864	88
1906–1915	36,526.4	1,528	2.185	103
1916–1925	88,896.6	3,720	2.482	117
1926–1935	178,075.1	7,451	2.021	95
1936–1945	172,236.7	7,207	2.669	125
1946–1952	134,049.3	5,609	3.183	149

Source: Data from Hokkaido Prefectural Office.

TABLE II

RATIO OF DIRECT-SOWN AND TRANSPLANTED RICE PADDY FIELDS IN HOKKAIDO

YEARS	DIRECT-SOWN RICE PADDY FIELDS	TRANSPLANTED RICE PADDY FIELDS USING NURSERY-GROWN SEEDLINGS	TRANSPLANTED RICE PADDY FIELDS USING SEEDLINGS GROWN IN OIL-PAPER COVERED FRAMES OR IN HOTBEDS
	per cent	*per cent*	*per cent*
1893	0	100.0	0
1906	28.0	72.0	0
1916	64.8	35.2	0
1926	81.3	18.7	0
1942	64.2	23.2	12.6
1953	26.3	9.6	62.4

Source: Data from estimates made by Y. YOSHINO and T. HOSHINO, of Hokkaido National Agricultural Experiment Station.

A CENSUS OF THE INSECT PESTS OF THE RICE PLANT IN HOKKAIDO

According to my recent census, 93 species of insect pests of the rice plant are distributed in Hokkaido (9). But only 50 species are regarded as injurious to the rice plant in the island. Among those hitherto recorded the following species may be ranked as comparatively serious and decidedly important:

I. Injurious to young rice plants or seedlings.
  a. Injurious in direct-sown paddy fields.
    1. Rice caddis-fly, *Setodes argentata* Matsumura
    2. Black-dotted caddis-fly, *Oecetis nigropunctata* Ulmer
    3. Rice midge, *Chironomus oryzae* Matsumura
  b. Injurious in both rice nurseries and paddy fields.
    4. Smaller rice crane-fly, *Tipula latemarginata* Alexander
  c. Injurious in oil-paper covered frames or in hotbeds.
    5. Larger iris cutworm, *Gortyna leucostigma* Hübner

II. Injurious to rice leaves.
  a. Cuts off or chews leaves.
    6. Rice curculio, *Echinocnemus squameus* Billberg
  b. Feed on leaves.
    7. Rice leaf beetle, *Lema oryzae* Kuwayama
    8. Rice leaf miner, *Agromyza oryzae* Munakata
    9. Rice green caterpillar, *Naranga aenescens* Moore
    10. Grass leaf roller, *Cnaphalocrocis medinalis* Guenée
    11. Rice-plant skipper, *Parnara guttata* Bremer et Grey
    12. Army worm, *Cirphis unipuncta* Haworth
    13. Yezo rice grasshopper, *Oxya yesoensis* Shiraki

III. Injurious by sucking on rice leaves and sheaths.
  14. White-spotted rice bug, *Eusarcoris lewisi* Scott
  15. White-back plant-hopper, *Sogota furcifera* Horvath
IV. Injurious by boring into rice stems.
  16. Rice stem borer, *Chilo simplex* Butler
  17. False rice curculio, *Notaris oryzae* Ishida
V. Injurious to rice ears.
  a. Feed on young ears before heading.
    18. Rice stem maggot, *Chlorops oryzae* Matsumura
  b. Feed on ears after heading.
    19. Northern rice katydid, *Homorocoryphus jezoensis* Matsumura et Shiraki

The absence is noteworthy in Hokkaido of the major rice pests found in the southwestern regions of Japan as well as in the Palaeotropics and the South Pacific Islands, such as the paddy borer, *Schoenobius incertellus* Walker, purplish stem borer, *Sesamia inferens* Walker. green rice leaf hopper, *Nephotettix bipunctatus cincticeps* Uhler, zigzag-striped leaf hopper, *Deltocephalus dorsalis* Motschulsky, black rice bug, *Scotinophara lurida* Burmeister, rice stink-bug, *Lagynotomus assimulans* Distant, rice bug, *Leptocorisa varicornis* Fabricius, slender rice bug, *Cletus trigonus* Thunberg, and other species.

Changes of Predominant Rice Pests with Changes in Culture Methods

In 1897, a sudden outbreak of the leptocerid caddis-fly (*Setodes argentata*) was reported from the direct-sown rice paddy fields in the vicinity of Sapporo (11). Previous to that time only slight injuries of the white-back plant-hopper (*Sogota furcifera*), rice stem borer (*Chilo simplex*), or certain other insect pests had been known, excepting somewhat noticeable injuries by the rice leaf-beetle (*Lema oryzae*) in Kameda County, the southernmost part of the island (11). Since then injuries by the larvae of this caddis-fly and also by those of the black-dotted caddis-fly (*Oecetis nigropunctata*) have been reported every year from all areas where the direct-sown paddy fields exist. The larvae feed on the roots of young rice shoots; these caddis-flies were for forty years at the head of major rice pests in Hokkaido (5). Though these insects are distributed widely over Hokkaido, Honshu, Kyushu, Korea or northern Manchuria, injury occurs rarely in the direct-sown fields in trial, except in Hokkaido and northern Manchuria, where rice culture through direct-sown method is practised. In Hokkaido similar injuries by the limnophilid caddis-flies, such as *Limnophilus correptus* Maclachlan and *L. amurensis* Ulmer were often reported in the direct-sown paddy fields in the northern areas (5). Serious injuries by these pests continued up to about 1943, though varying from year to year, but since then the damage has shown a tendency to decrease gradually, corresponding with the reduction of the acreage of direct-sown paddy fields. The correlation coefficient between the acreage of infested paddy fields by the caddis-fly larvae and the acreage of oil-paper covered frames and hotbeds which grow the rice seedlings, between 1941 and 1952 inclusive, is $r = -0.915$ ($P<0.01$).

The rice leaf beetle (*Lema oryzae*) which had been restricted only to the Oshima Peninsula, southern Hokkaido, extended its habitat to neighbouring areas, with the bringing in of rice seedlings from the peninsula in 1914, due to the scarcity of rice seeds after the bad harvest of the previous year. From 1921 this beetle obtained a foothold here and there in the northern areas of Hokkaido, and then rapidly extended its infestation centrifugally from those points (2, 4). According to information from the Hokkaido Prefectural Office in 1930, the paddy fields infested by this pest were estimated at as high as 65 thousand hectares in Hokkaido. This pest, in both its adult and larval stages, does harm to the rice plant by gnawing out longitudinal strips from the leaves, and in severely infested cases a stretch of the infested rice field loses its lively green colour, giving the appearance of having been burned by fire as far as the eye could see (3). Such severe ravages continued until about 1945, then decreased gradually. It must be noted that this trend of prevalence coincides with the variation in the acreage of paddy fields. Also this conspicuous decrease of paddy fields infested by this pest in recent years was accelerated by the extension of control measures using calcium arsenate as devised by me (4). The correlation coefficient between the acreage of paddy fields infested by the rice leaf beetle and the total acreage of paddy fields in Hokkaido from 1941 through 1952 is $r = +0.769$ ($P<0.01$).

Simultaneously with the decline in ravages of the rice leaf beetle, infestation by the rice leaf miner *(Agromyza oryzae)* increased particularly since 1941. The larva mines into the rice leaf making an irregular tunnel, and as a result of this injury the leaves wither as if burned by fire.

These phenomena seem to be due to "arena" of competition or "the lists" between two leaf-feeding insects above noted. In addition to the damage by these predominant pests, severe injuries from the chewing of the young rice leaves by the rice curculio (*Echinocnemus squameus*) were sometimes noticeable from 1940 to the present time, especially in the central areas of rice culture. When severely infested, all of the rice leaves above the surface of water are lost as if clipped off. This pest is widely distributed from Hokkaido in the north to Formosa or Java in the south. In Hokkaido it produces only one generation annually; when the summer temperature is high, it completes its life cycle to the adult stage and easily overwinters, but when the summer is cool the larger part of the insect population overwinters in the larval or pupal stages, of which the mortality during hibernation is very high. Thus, in the year following a summer of unseasonable weather the population of this pest decreases, and the injuries have a corresponding tendency to diminish.

As stated above a recent important advance in culture methods since 1935 lies in the development and promotion of a method making use of rice seedlings grown in oil-paper covered frames or in hotbeds. Meanwhile, a new insect pest, the large iris cutworm (*Gortyna leucostigma*), has appeared here and there in these frames or hotbeds, boring into young shoots of rice seedlings at the ground surface level (6). Sometimes 50 per cent of the seedlings in one frame were withered down by this pest. The larvae, however, can not develop to a full-grown instar in the rice plant, and consequently the injury on the rice plant may be regarded as temporary.

With further extension of the use of transplants from oil-paper covered frames or hotbeds, the rice stem borer (*Chilo simplex*) has become the leading pest. This very serious pest is adapted to the north temperate climate by the production of only one generation a year; it often prefers the broomcorn millet (*Panicum miliaceum*) as an alternate food plant when the rice plant is not available for is scarce (10). In reality this pest has been known for a long time and severe injuries have been occasionally noticed in warmer years, but the injuries in recent years are conspicuous and rapidly spreading parallel to the extension of the transplanting method above described. The correlation coefficient between the acreage of paddy fields infested by this pest and the acreage of oil-paper covered frames and hotbeds which grow the rice seedlings during the period 1941–1952 inclusive is calculated as $r = + 0.718$ $P<0.01$). The reason that the injuries are expanded may be due to accelerated growth or "phase" of rice plants as influenced by the change in culture method.

SOME CONTROL MEASURES ADOPTED IN THE RICE CULTURE IN HOKKAIDO

Since the larvae of caddis-flies live at the bottom of the irrigation-water and breathe through tracheal gills, spraying with ordinary contact or stomach insecticides is not effective, because the water acts as a barrier. So, a dry-sand sprinkling method was devised and it has been used by farmers. Dry-sand mixed with either pyrethrin-extract in kerosene or insect powder is sprinkled over the paddy field where the water had previously been drained low. By these means, kerosene or insect powder may be deposited with the sand without dilution at the bottom of water, where the insecticide comes in effective contact with the larvae. It is necessary to change the water within two or three hours after the application. Recently I found through experiments that putting the ethyl ester of cocoanut-oil fatty acid containing pyrethrins into the irrigation water is also effective (7). It must be noted that transplanting methods through the use of both nursery-grown seedlings and the seedlings grown in oil-paper covered frames or hotbeds can eliminate the injuries.

Against the rice leaf beetle the following procedures were recommended and practised before 1934: collection of the egg-masses, liberation of egg-parasite (*Anaphes nipponicus* Kuwayama) by use of the so-called "protecting apparatus of natural enemies" when it is found, brushing off with boat-shaped net, and spraying with contact insecticides such as pyrethrum-soap solution. However, the serious ravages by this leaf beetle led me to carry out further investigation and after repeated trials, it was found that calcium arsenate is the most effective stomach insecticide and in 1935 its application was recommended (4). Within a few years this practice was extended over the larger part of infested paddy fields on the confirmation by farmers of its effectiveness. In recent years better results with DDT or BHC have been reported.

Control of the rice leaf miner is one of the difficult problems. Of three recommended measures, viz., spraying with contact insecticides, collection of the overwintered puparia before their emergence as adults in the spring, and eradication of *Zizania latifolia*, a potential wild host, spraying is the most effective. From the results of my laboratory tests and field experiments it has been concluded that derris emulsion, followed by derris powder, is consistently the most efficacious against this pest, as against either nicotine sulphate or pyrethrum (8). More recently, DDT, BHC and other synthetic organic insecticides have been experimented with, but the results so far have been inconclusive.

As regards control of rice curculio, reduction of the injury by transplanting the seedlings which were nursed in oil-paper covered frames or in hotbeds, mixing pyrethrins-extracted kerosene into mud during harrowing time, fall ploughing, collecting the beetle with the aid of attractants, such as mixture of molasses, Japanese wine, and vinegar, or through the use of a bundle of straw, sprinkling pyrethrin-extracts in kerosene on water in rice paddies and sweeping rice plants with rope, causing beetles to jump from the plants into the kerosene film where they are killed, have been hitherto recommended. Recent experiments, however, proved that dusting with BHC is fairly effective against the beetle. This measure is now extensively practised by farmers.

Against the rice stem borer, methods such as catching the moths, collection of egg-clusters, protection or liberation of egg-parasites and so on can not be employed in Hokkaido, as the infestation does not occur here during nursery season. It is recommended to cut the straw as low as possible at harvest and to make careful barn-preservation of the straw during the next season of emergence. Trapping moths with blue fluorescent lamp is now carried out in southern Japan, but that practice can not be adopted generally in Hokkaido. However, it shows fair effectiveness in warmer districts of the island as it does in southern Japan (1, 10). However, in many cases, effective results through the trapping with incandescent lamp before emergence of the moths from the straw which has been preserved in barn, have been recorded; this measure is now practised by many farmers (1, 10). Application of insecticides against the rice stem borer has been considered as undependable in effect, but quite recently marked effectiveness with parathion, especially with Folidol-E605, was proved by many research workers in Japan. Also in Hokkaido dusting of parathion as well as that of BHC $r3\%$ throughout the period of moth-flying, egg-laying, and first larval stage, that is from mid-July to early in August, have been found effective, especially through the efforts of K. Endo and K. Nakamura of the Hokkaido Prefectural Agricultural Experiment Station. Their excellent results are now being translated into practice by farmers in Hokkaido (1).

Finally, I wish to express my heartfelt gratitude for the friendly encouragement and kind assistance which Prof. Dr. L. B. UICHANCO of the Philippines has extended to me during the preparation of this manuscript.

LITERATURE CITED [1]

1. ENDO, K., K. NAKAMURA, *et al.* 1953: Experiments on Organic Phosphorus Insecticides against Rice Stem Borer. [Spec. Publ. by Hokkaido Pref. Office]
2. KUWAYAMA, S. 1928: The Principal Insect Pests of the Rice Plant in Hokkaido [*Bul. No. 47, Hokkaido Agr. Exp. Sta.*]
* 3. ———— 1932: Studies on the Morphology and Ecology of the Rice Leaf Beetle, *Lema oryzae* Kuwayama, with Special Reference to the Taxonomic Aspects. [*Jour. Facul. Agr., Hokkaido Imp. Univ.*, Vol. 33, No. 1]
4. ———— 1932-'37: Studies on *Lema oryzae* Kuwayama, the Rice Leaf Beetle. Pts. I-VII [Rep. Nos. 29, 33, 37, 38, *Hokkaido Agr. Exp. Sta.*]

---

[1] All are written in Japanese, excepting the articles marked with an asterisk.*

5. KUWAYAMA, S. 1934: On the Life History of Two Species of Leptocerid Caddis-Flies Injurious to the Rice Plant. [*Trans. Sapporo Nat. Hist. Soc.*, Vol. 13, pt. 3]

6. ———— 1944-'45: Supplements to the Knowledge of Insect Pests of the Rice Plant. [*Agr. & Hort.*, Vol. 19, No. 12; Vol. 20, Nos. 1, 2, 3]

7. ———— 1947: Value of the Ethylester of Fatty Acid as an Insecticide Put into the Irrigation Water. [*Nogaku Soho* (Agr. Bul.) *Fasc.* 3, pt. 2]

8. ———— 1950: The Rice Leaf-Miner: Some Observations on its Ecology and Experiments along the Control Measures. [*Trans. Eighth Int. Congr. Ent.*]

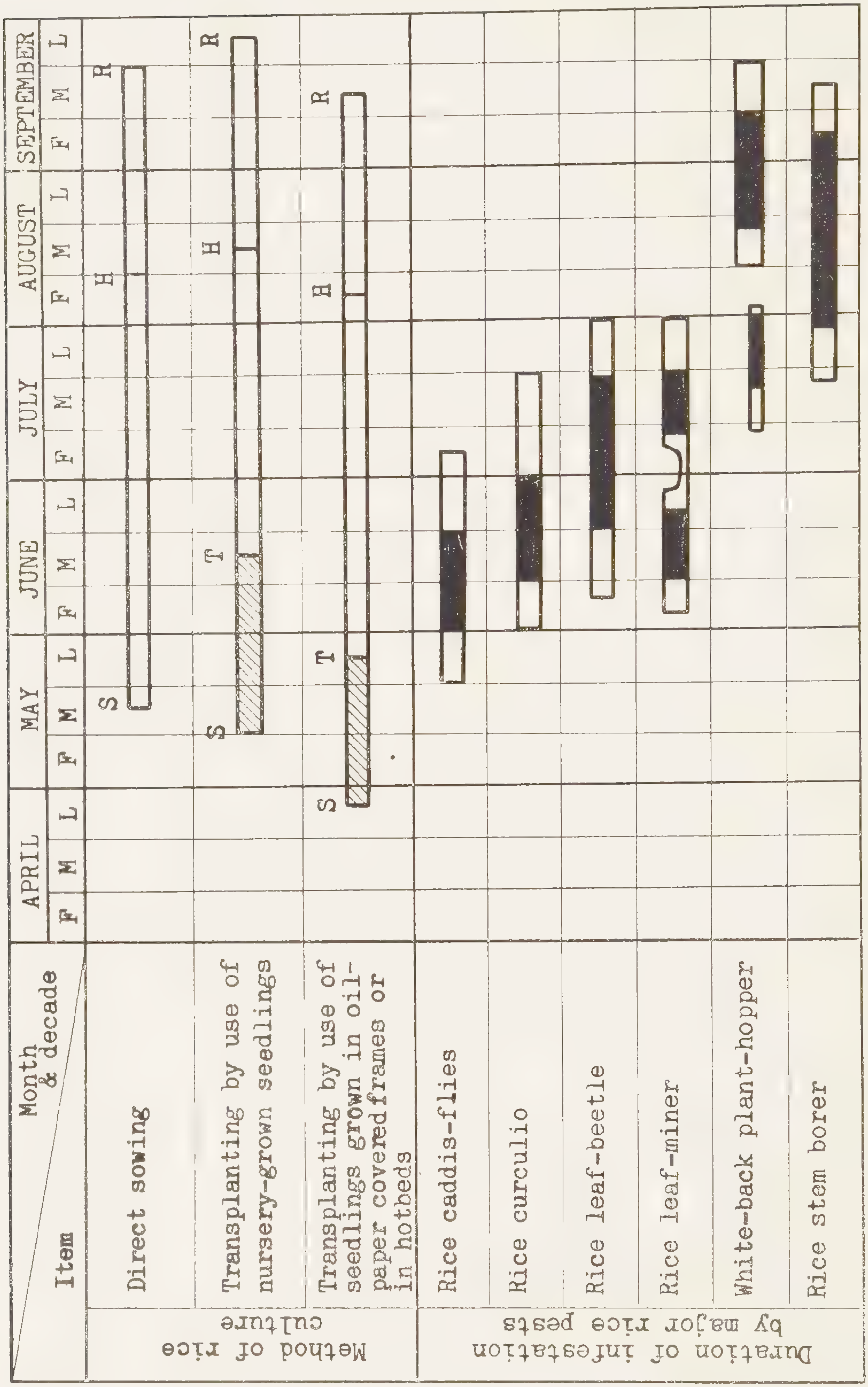
9. ———— 1952: On the Fauna of Insects Injurious to the Rice Plant in Japan. [*Trans. Ninth Int. Congr. Ent.*, Vol. 1]

10. ———— and K. ENDO. 1952: Rice Stem Borer in Hokkaido. [Materials for Agr. Ext. No. 12, Hokkaido Pref. Office]

11. MATSUMURA, S. 1897: On the Insect Pests of Rice Plants in Hokkaido. [*Hokkai no Shokusan* (Plant Indust. in Hokkaido), Vol. 8, No. 96]

12. NARITA, T. and D. IKE. 1953: Materials for the Prediction of Prevalence of Rice Stem Borer. [Spec. Publ. by Hokkaido Pref. Office]

13. NUTTONSON, M. Y. 1951: Ecological Crop Geography and Field Practices of Japan. Japan's Natural Vegetation, and Agro-climatic Analogues in North America. [Publ. from *Am. Inst. of Crop Ecol.*]


Item
Month & decade
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
F
M
L
Method of rice culture
Direct sowing
Transplanting by use of nursery-grown seedlings
Transplanting by use of seedlings grown in oil-paper covered frames or in hotbeds
S
T
H
R
Duration of infestation by major rice pests
Rice caddis-flies
Rice curculio
Rice leaf-beetle
Rice leaf-miner
White-back plant-hopper
Rice stem borer

November 18, 1953

Presiding: Dr. Henry A. Bess, Department of Entomology, University of Hawaii, Honolulu 14, Hawaii, U.S.A.

Secretary: Dr. Silverio M. Cendaña, College of Agriculture, University of the Philippines, College, Laguna.

PROCEEDINGS

The following papers were read:

1. Given, B. B. Observations on Behavior of Australian Thynninae. (Abstract on page 127 of Abstract of Papers.)

The paper was read by Dr. Townes in the absence of Dr. Given. Discussion followed the reading of the paper.

2. Haramoto, Frank H. Observations on the Biology of *Opius oophilus* Fullaway (Braconidae–Hymenoptera). (Abstract on page 128 of Abstracts of Papers.)

The paper was read by Dr. Bess in the absence of the author. Discussion followed the reading of the paper. The desirability of importing *Opius oophilus* into the Philippines for fruit flies has been pointed out by Dean Uichanco.

3. Uichanco, L. B. Occurrence and Nature of Explosive Outbreaks of Various Insect Pests in the Philippines. (Abstract on pages 130–132 of Abstracts of Papers.)

A lively discussion followed the reading of the paper, chiefly on the migratory locust.

Some of the discussions follow:

Dr. Townes: My impression is that the permanent breeding grounds is not very thickly covered with grasses. After the swarms have built up, the locusts go to areas more thickly covered with grasses such as cogon. The marshes are covered with grass.

Dr. Bess: Why do those outbreaks come up, why do they go down?

Dean Uichanco: We should possibly go to Uvarov's theory of phases, although I differ from him with regards to the reversibility of the phases. In the Philippines, the periodicity of swarming apparently bears a negative correlation with the sunspot cycle, on account of the effect of solar activity on the climate in the breedy areas.

Dr. Bess: Could it be diseases in connection with sunspots?

Dean Uichanco: Possibly a complex of factors.

Dr. Townes: The general pattern of swarms is that they begin to build in July, reaching the peak in September and October.

Dr. Bess: Does the outbreak last a number of years?

Dean Uichanco: There have been records during Spanish times of swarms persisting through as long as 10 years.

Dr. Townes: There are some Bureau of Plant Industry men here who just came fresh from the fields. Can we hear from them?

Mr. Toquerro: It is true that Cotabato is one of the permanent breeding places of the migratory locust in the Philippines.

Dr. Bess: Dr. van Steenburgh has pointed out that observations of 15 years duration in forest insects (in Canada) revealed some limited areas in which general infestation occur year in and year out, and from these points, infestations of bigger areas occur under favorable conditions.

Dr. Pemberton: Prior to introduction of parasites on army worms in Hawaii, we had periodic intense, really intense, outbreaks of army worms. Since 1942, when another complex of parasites was introduced, there have been no more serious outbreaks.

Dr. Cendaña: We have two principal parasites of armyworms in the Philippines, *Chelonus* sp. and a tachinid fly. The recurrence of serious outbreaks possibly points out to the need of importing more parasites.

Dr. Bess: We will be glad to help.

4. VAYSSIERE, P. Sur les Parasites de l'*Elaeis* et de l'*Hévéa* dans la Peninsule de Malacca.

In the absence of the author, the paper, which was in French, was summarized in English by Dr. Boschma.

There was not much discussion on the paper.

5. SISON, PEDRO. Further Studies on the Biology, Ecology and Control of the Black Beetle of Coconut, *Oryctes rhinoceros* Linn. (Abstract on page 152 of Abstracts of Papers.)

It was agreed to have the discussion on this paper until the other papers dealing on this insect have been read.

6. GRESSITT, J. L. Rhinoceros Beetles as Pests of Coconut Palms. (Abstract on page 133 of Abstracts of Papers.)

The paper was read by the author. Colored lantern slides showing damage by the beetles were projected.

7. Dumbleton, L. J. The Rhinoceros Beetle as a Regional Problem in the South Pacific. (No abstract.)

It being already lunch time, it was decided to recess and to reconvene at 2:00 o'clock, at which time the discussions on the Oryctes beetle will be held and the rest of the papers for the day read.

8. O'Connor, B. A. Notes on *Oryctes rhinoceros* Linn. in Fiji. (No Abstract.)

The paper was read by Dr. Gressitt (in the absence of the author).

It was suggested that the paper by Dr. Gardner on the beetle be read at a later session because he had not arrived yet.

There was a long discussion on the *Oryctes* beetle. Part of it follows:

Dr. Pemberton: It would possibly be more interesting to know how much the beetle could increase in, say, 5 years.

Dr. Gressitt: Three years after it was introduced in Samoa 23,000 adults were collected.

Mr. Coolidge: This problem brought up the possibility of cooperation among countries in which the beetle is found and is a menace, specifically from countries in which the pest has long been established to those in which the pest has been newly introduced.

Dr. Bess: What is your estimate, Dr. Owen, of the effectiveness of your clean-up work?

Dr. Owen: This is very hard to answer. The task of cleaning up is big because there are plenty of palms and dead trees.

Dr. Bess: How important is that work? Suppose after cleaning up, say 2 or 3 years, could you recommend planting of new trees?

Dr. Owen: It might help.

Dr. Bess: How old will palms have to be to be attacked by the beetle?

Dr. Owen: Possibly 3 or 4 years.

Mr. Coolidge: I wonder whether the lessened number of the pest (in countries where it is an established species of long standing) is due to sanitation, as (is claimed) in Java.

Dean Uichanco: The pest has not been very serious (in the Philippines) so we have not paid much attention to it.

9. Newell, Irwin M. Small-Sample Techniques in the Analysis of Fruit Fly Population Phenomena. (Abstract on page 134 of Abstracts of Papers.)

The paper was read by Dr. Bess.

10. CENDAÑA, S. M. and NAMOCALE, P. P. A Biological Study of *Bactrocera umbrosa* (Fabricius) (Trypetidae, Diptera). (Abstract on page 136 of Abstracts of Papers.)

The paper was read by the senior author.

11. GARDNER, T. R. Observations on the Rhinoceros Beetle *Oryctes rhinoceros* in Malaya.

12. SÉGUY, E. Sur les Coléoptères Lucanides des Philippines Note sur leur Chorologie. (Abstract on page 24 of Supplement to Abstracts of Papers.)

The paper was read by Dr. Boschma.

OBSERVATIONS ON BEHAVIOR OF AUSTRALIAN THYNNINAE

By B. B. Given
Entomological Research Station, Nelson, New Zealand

Introduction

The observations herein recorded were made while engaged upon a search in Australia for parasites of Melolonthinae suitable for shipment to New Zealand for use against the endemic pest, *Costelytra zealandica* (White). Consequently, these notes are based on restricted numbers of species in a restricted area. However, in some aspects, they cover a wide range of thynnid type, including members from each of the three tribes *Diammini, Thynnini,* and *Rhagigasterini.* Within the major tribe (*Thynnini*) they cover the two basic groups of genera, *Tachynomyia* on the one hand and *Thynnoides, Hemithynnus* etc. (the major genus *Thynnus* of Turner 1907–1908) on the other.

Many of these observations are incomplete, but as it is doubtful if the writer will have the opportunity to pursue them further, they are recorded as a basis for future workers in this field. Basic observations on the subfamily have been recorded by Burrell (*Journ. N. Y. Ent. Soc.,* Vol. XLIII, 1935), and aspects dealt with by him are not repeated in the present work. Where further information on these aspects has been noted, or where disagreement occurs, results of observations are given. The nature of female feeding in association with structural modification of both sexes, forms the basis of a further paper and is not dealt with in detail here.

General conclusions on population trends are based on field observation and surveys of material in collections. Data on more specific or restricted aspects of behavior are based solely on observation in the field.

Population and Sex Ratio

The pattern of population fluctuation and sex ratio is far from constant over all genera or species of the *Thynninae.* However, the most important divergence from the normal pattern appears to be exhibited by the species *Diamma bicolor* of the tribe *Diammini.* This insect is remarkable in many ways, and bears no close affinity to any other thynnid or to any other group of fossorial wasps.

The pattern of population trend and sex ratio as illustrated in Figure 1A is believed to be basic to the majority of species. The pattern is based on *Thynnoides gracilis* (?), a very common species in Victoria. The actual sex ratio appears to be normally almost equal, but the apparent ratio varies considerably according to the time in the season and the section of the environment observed. These sections of the environment are:—

1. the breeding area above ground
2. the breeding area below ground
3. the adult feeding area, and
4. sheltering areas (overnight, or under adverse conditions).

Figure 1A is self-explanatory, but it is as well to point to the significance of the various phases. Males normally emerge first, couple with females as the latter appear, stay with the females until feeding and mating is complete, then return females to the breeding ground for oviposition. After some time at the breeding ground, during which 6 to 10 eggs may be laid, females emerge for fresh coupling, feeding, and possible mating. At the conclusion of the season, only males are seen at the feeding-ground, and all surviving females are beneath ground-level. During the active mating season, pairs frequently remain coupled overnight.

The divergent pattern of *Diamma bicolor* is illustrated in Figure 1B. In this case, males emerge in very large numbers during the latter half of October in Victoria, and after feeding, range over breeding-grounds for emerging females. The point from which the female is about to emerge becomes a seething mass of males, digging to assist her exit from the soil. The female rapidly crawls towards the nearest tree in bloom, and after travelling some distance appears to select a male. Mating appears to occur once, and the female thereafter is independent of the male. Female longevity appears to be considerable, as in areas where no males are to be seen after early November, females are present late in January. In the sub-alpine area of Kiandra in New South Wales (elevation 4,500 ft.) females are present in numbers in March and possibly later. The male of this species has been described as rare, but this is far from the truth during their flight period. From field observations, it would appear that the sex ratio actually favours males.

A further abberration in pattern apparently exists in the case of the genus *Tachynomyia*. In this genus, it would appear that males greatly outnumber females, or in some species that females are almost non-existent. However, in actual fact the numbers of each sex are usually very well matched in this genus. The apparent discrepancy is due to the fact that females in many species are almost always fed by males at or near the breeding-ground. This also applies to *Hemithynnus apterus* and to several other species of various genera. Some of these species are able to travel surprising distances between feeding and breeding grounds, and in the case of a large species of *Tachynomyia* (probably not described) the males of which were observed in large numbers for several seasons, females were never taken or seen, despite surveys of surrounding country for a radius of several miles. The structural modifications in this species to serve the purpose of nectar transport, are carried to a state of surprising perfection.

The local nature of many populations is a further remarkable aspect of thynnid behavior, and it would appear that migration of adults from feeding ground to breeding ground is governed by some form of inherited "memory" or instinct. In the case of *Thynnoides gracilis* (?), which was under observation for five years at Cavendish in Western Victoria, a surprising case of this type of behavior was noted. On a roadside *Leptospermum* area, these thynnids swarmed in mating and feeding pairs. The breeding ground was eventually located three quarters of a mile away, bordered by a further patch of *Leptospermum*. However, very few *Thynnoides* were found on this second *Leptospermum*, despite the fact that it appeared to be extremely attractive to other nectar-feeders, including several thynnid species. However, the first area of blossom was much older than the second, and on investigation it was found that a regular aerial route existed between breeding and feeding ground, passing directly above the younger *Leptospermum* area. It was noted that *Hemithynnus apterus* behaved in a similar manner in the same area.

Further evidence of this remarkable habit was noted at Wannon, a nearby district, during the collection for consignment to New Zealand of a variety of thynnid species. During the spring of 1947, a range of species was noted feeding at scale infestations (*Eriococcus coreaceous*) over a relatively wide area. This scale was at the time diffuse in distribution, and the thynnids were distributed correspondingly. During the spring of 1948, scale infestations were more restricted due to parasitism, and the thynnid population was correspondingly concentrated. By the following spring, no scale could be found, and honey-water spraying was resorted to with striking results. At first, three trees forming the points of an equilateral triangle of approximately 100 yards side were used. Results were not markedly different at the three trees, but one was finally selected for all collecting on account of its convenience. Collecting from this tree was intensive during the months August-November in 1949, 1950 and 1951. In 1950, other trees sprayed in the neighbourhood showed little attraction to thynnids, although blow-flies and honey-bees were attracted. By spring of 1951, it was almost impossible to induce any thynnids to feed anywhere but at the original tree. This observation held good at various times during the season, and even when the original tree was honeyless, it was some time before any wasps appeared at any other sprayed tree, and then the population was relatively low. The numbers of thynnids visiting this tree during the height of the season (October) was very great, probably in the nature of tens of thousands of pairs per morning, while the number of different species collected from it was approximately 30 in 1951.

The collecting tree at Wannon was an ideal field laboratory for observation purposes. Unfortunately at times when most observations should have been made, it was imperative to spend all possible time on the selection and mass collection of thynnids for consignment to New Zealand. Local population trends on this tree illustrated several interesting facts, but many of the observations on these trends are too incomplete to be worthy of more than passing mention.

Gregariousness

This subject can be readily divided into three categories on the basis of observations made. Had it not been for the fact that large adult populations concentrated by the use of sprayed honey in the absence of good supplies of natural food were available for study, these observations could not have been made. The three main categories under which this subject falls, are as follows:—

(a) At the breeding ground.
(b) At the feeding ground.
(c) Under adverse conditions.

At the breeding ground, causes of gregariousness are obvious. Host populations tend to exist in concentrations, and this naturally draws the parasites. However, this aspect is one which requires some comment, as it is usually not as simply logical as would appear. As an example, we may consider the aphodiid host, *Aphodius howitti*. This insect is at times a major pest of high grade rye-grass and clover pasture in Australia, yet rarely if ever is it parasitised where populations are in epidemic proportions. These epidemic populations are markedly unstable and usually transient. However, there is frequently a relatively stable *Aphodius* population in this native pasture in open tall scrub ("stringy-bark" etc.) country, and under these conditions parasitism by a species of *Tachynomyia* sometimes reaches over 80% and is fairly generally present, at least in southern Victoria. This I assume to indicate the scrub habitat to be the primitive one, and that the host but not its parasite, has become adapted for life (under certain conditions) in improved and sown open pasture. It appears to be the case with other thynnid species also, that populations in the soil are highest among native grasses. For example, among native tussock patches in sown pasture, populations are invariably higher than in the foreign pastoral components. Exceptions probably occur in some cases, and old strawberry beds appear to present such a case.

At the feeding ground, congregation is primarily dependent on the area of the food source. However, when "leaf-curtains" are uniformly sprayed with honey-water, some unexpected results are noted under high population conditions. The first intimation of any irregularity was noted when two collectors were operating on different sections of a tree, and obtained quite different compositions to their collections. It was first thought that this lack of uniform distribution was due to selective action of physical conditions. This was only partly true, as further observation proved. Several species were observed, and it was noted that some showed no signs of gregariousness, while others did, in both space and time. The first arrivals of one species noted appeared to fly in together, and others arriving settled near them forming a definite species aggregation. This tendency was noted in several species, although in all cases there were specimens which did not conform to the general pattern. In some species, this habit does not appear to be at all evident, but may be merely less strong. It is possible that this habit may explain the seasonal visiting of thynnids to a particular food source. The source may be the first attractive one after emergence, causing the early emergents to visit it, passing on the habit by virtue of gregariousness of feeding habits.

Under adverse conditions and at night, gregariousness is often evident in males, and if they are coupled at the time, the females are taken with them. The normal habit of many species in the late evening is to return to the breeding ground, where they settle on grass stems or blades a few inches above ground. If overtaken by adverse conditions during the night, they drop and crawl into the bases of the pasture plants. However, in one species in particular (unfortunately not at present identified), the night is often spent near the feeding ground, and gregariousness is very evident. Under sudden adverse conditions this habit is even more marked. On one occasion, when a sudden cold wet spell overtook the local population, a survey was made and aggregations of this species were noted, particularly in hollowed stems of *Xanthorrhoea* sp. In one case, in 3 inches of hollow dead flower stem, were noted 19 males, 2 coupled with females. In no case did any stem contain only a single male, and about one stem in 10 contained wasps.

A rather curious form of gregariousness has also been observed when among large populations of *Hemithynnus* spp. This is particularly evident with *H. apterus*. The feeding males, when disturbed, concentrate about a foot above the head of the observer, flying in a figure-8 course at great speed. The effect is much the same as with a disturbed beehive, and is probably an effort at disconcertion.

Reaction to Temperature

Observations on temperature reactions are restricted to certain species which fly during the spring in Victoria. These observations are incomplete, but nevertheless of some significance.

Emergence of the earliest-flying species observed in western Victoria does not commence until soil temperature at 2 inches (normal depth of cocoons) is over 12°C, and velocity of emergence of these species reaches a maximum for both sexes at somewhat over 22°C. However, this factor does not alone govern emergence (see next section and Figs. 2 and 3). The species concerned can at present be designated only by the index numbers used when collecting them, and those referred to above are 19, 20, and 46. Species 24 commences emergence at approximately 13°C, and species 66 at a slightly higher level. Many other species emerge only at much higher temperatures. Air (shade) temperatures of about 15°C or over are necessary for any marked activity at feeding sources. At this stage, species 19, 20, 24, 25, 46, 66, and 75 become quite abundant.

During the spring, very rapid climatic changes are frequent in south-western Victoria, and during such changes, reactions were observed with great interest. Several times, reactions to a drop in shade temperature from 20°C to 12°C and the corresponding temperature rise, have been observed, with particular reference to species 24.

Normal activity is maintained during dropping temperature to about 16°C. At 15°C activity is markedly reduced at 13°C flight becomes impossible for mating pairs, and at 12°C all wasps drop to the ground where they remain immobile. At this stage, a rise of 1°C produces activity, and at 14°C flight is possible.

Reactions to Humidity

Little is known of reactions to relative humidity, as records were not taken. However, certain data are available concerning the influence of soil moisture on emergence, and these are illustrated in Figures 2 and 3. It will be noted that emergence of species 24 and 46 commenced after the first heavy spring rains, and species 66 emerged after later rains, in both seasons for which full records were kept. It will also be noted that the correlation between temperature and emergence is not as close as that between rainfall and emergence.

Overwintering is in the prepupal stage, and pupation is undoubtedly dependent on both temperature and soil-moisture. From pupation to adult emergence occupies probably about 2–3 weeks in most cases, and adult emergence is again dependent on temperature and soil-moisture combined. Material (prepupal) held at room temperatures under low humidity conditions has remained alive and unchanged for nearly 3 years while similar material held in a damp medium emerged within 1 year. One cocoon emerged after 3 years within a month of being placed on damp cotton-wool. The usual type of thynnid cocoon is spindle-shaped, but bluntly rounded at one end. The body of the cocoon is impervious to water, but at the narrow end is a somewhat flattened porous pad. This pad is normally in contact with one end of the earthern pupation chamber, while the body of the cocoon is held away from the earthern walls by a few loose silken fibres. It would appear that this porous pad acts as a moisture-conditioning organ for the interior of the cocoon. In *Diamma, Hemithynnus,* and *Tachynomyia* this condition is absent or feebly developed and is possibly best developed in *Thynnoides.*

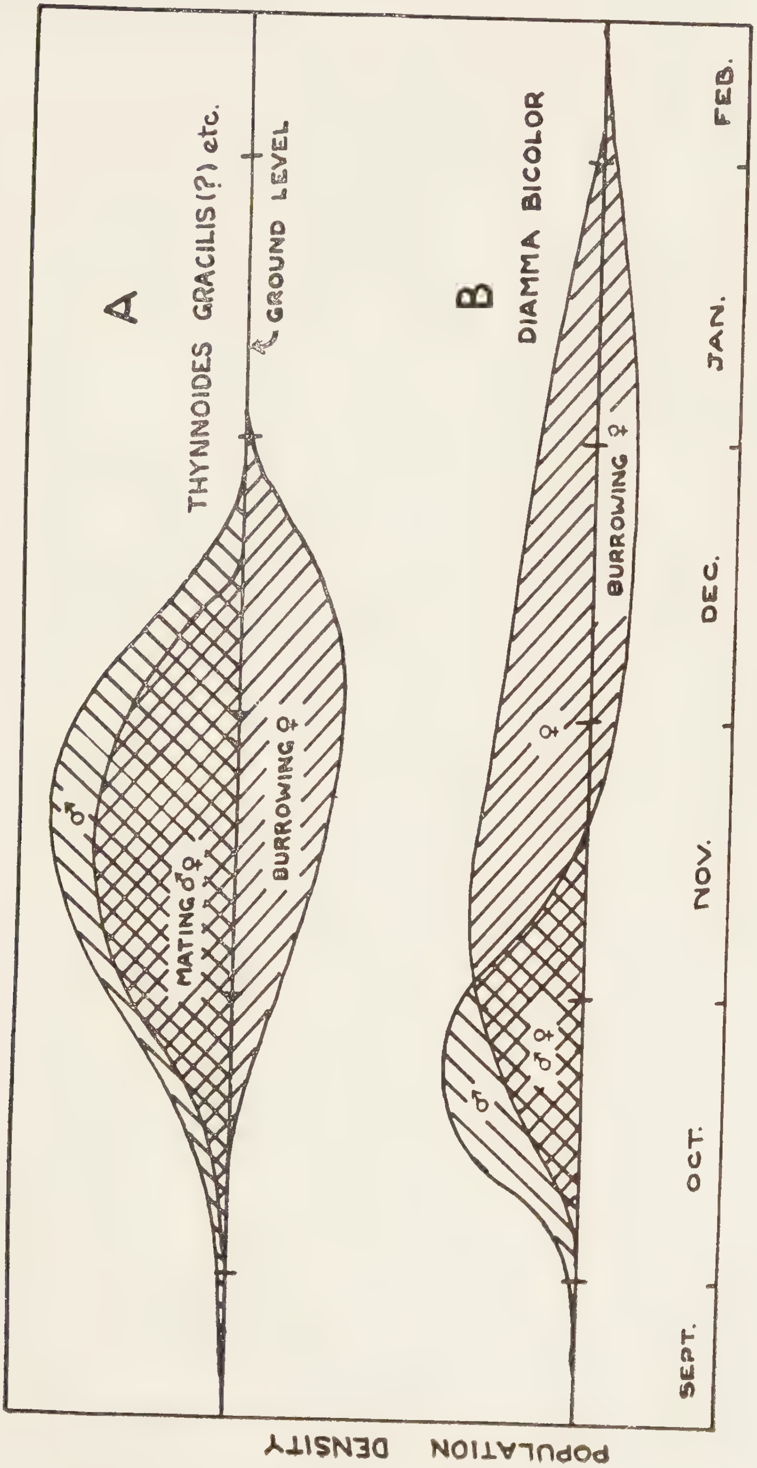
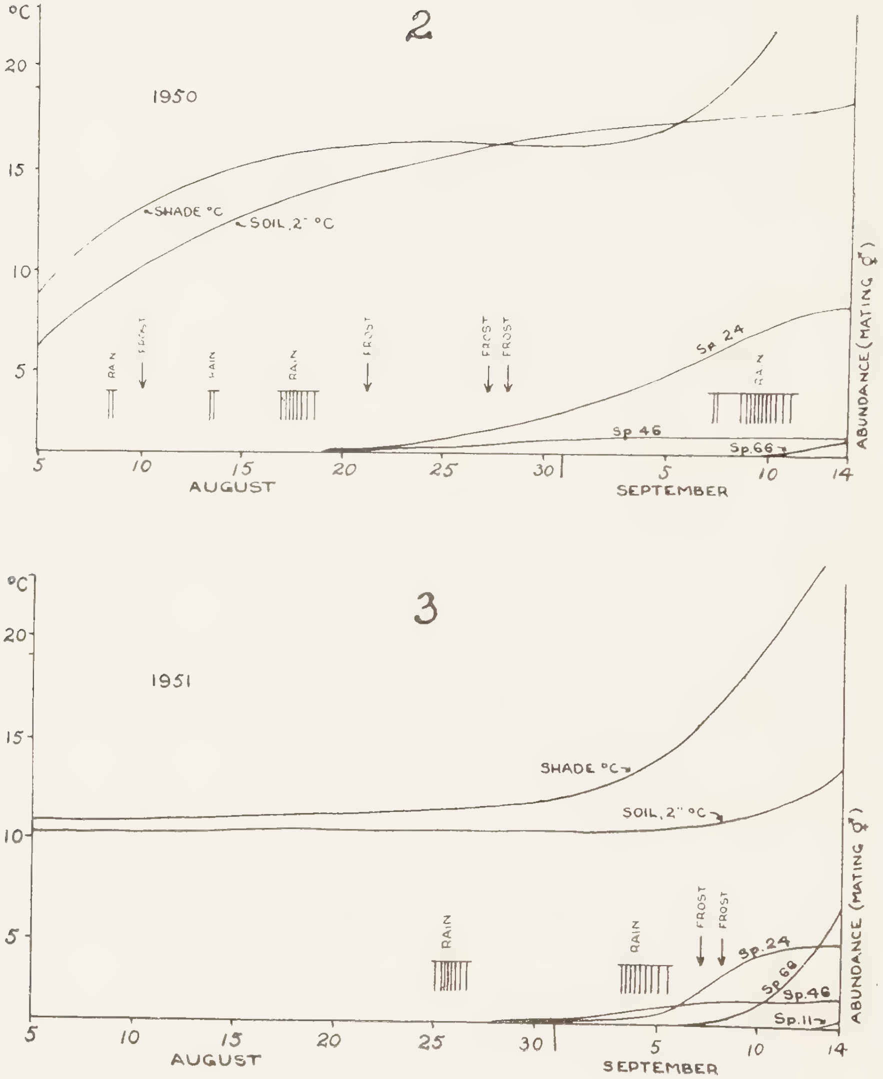

A
THYNNOIDES GRACILIS (?) etc.
GROUND LEVEL
♂
MATING ♂♀
BURROWING ♀
B
DIAMMA BICOLOR
♂
♂♀
♀
BURROWING ♀
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
POPULATION DENSITY

FIGURE 1



FIGURES 2 and 3

OBSERVATIONS ON THE BIOLOGY OF *OPIUS OOPHILUS* FULLAWAY (BRACONIDAE-HYMENOPTERA)[1,2]

By Frank H. Haramoto[3]
University of Hawaii, College of Agriculture
Agricultural Experiment Station
Honolulu 14, Hawaii

Introduction

The braconid parasite, *Opius oophilus* Fullaway, is an egg-larval parasite of the oriental fruit fly, *Dacus dorsalis* Hendel. It was the first opiine parasite of a fruit fly (Tephritidae-Diptera) found to have an egg-larval habit (van den Bosch and Haramoto, 1951).

O. oophilus was first obtained from *D. dorsalis* larvae reared from guava fruits, *Psidium guajava* L., collected at Waikane, Oahu, Territory of Hawaii, in December, 1949. Prior to 1951, *O. oophilus* was considered to be a "melanistic form" of *Opius vandenboschi* Fullaway, which was then the most common parasite of *D. dorsalis.* Soon after its discovery in December, 1949, this "melanistic form" spread rapidly over the entire island of Oahu and became so numerous that by July, 1950 it was the predominant opiine parasite of *D. dorsalis.* Critical morphological and biological studies (van den Bosch and Haramoto, 1951) revealed many distinct differences between the so-called "melanistic form" and the typical form of *O. vandenboschi* and consequently it was described as a new species (Fullaway, 1951).

O. oophilus is not a native Hawaiian species but is believed to have come from Malaya. It was apparently introduced and liberated in Hawaii as *Opius persulcatus* (Silvestri) in 1948 and 1949 (Bess *et al.*, 1950).

Although much is already known about the activities of *O. oophilus* because of the concentrated work done by the various agencies cooperating on the control of the oriental fruit fly (Carter, 1950), very little attention has been given by other workers on its biology. This paper presents some observations made on the biology of *O. oophilus.*

---

[1] Published with the approval of the Director of the Hawaii Agricultural Experiment Station as Technical Paper No. 298.

[2] Portion of a thesis submitted to the University of Hawaii in partial fulfillment of the requirements for the degree of Master of Science.

[3] The author wishes to express grateful acknowledgment to Drs. Henry A. Bess, Irwin M. Newell, Marion L. Lohman, and Robert van den Bosch, under whose guidance this study was conducted.

METHODS AND MATERIALS

O. oophilus adults were obtained by rearing parasitized *D. dorsalis* larvae from fruits collected in the field. Guava fruits were used most frequently because they are obtainable throughout the year and are considered as the major host of *D. dorsalis* in Hawaii (van den Bosch *et al.*, 1951). Observations of the adult behavior in the field were made in guava groves. Rearing data were obtained predominantly from guava fruits. The guava fruits infested with *D. dorsalis* larvae were brought into the insectary, the larvae were removed and transferred into blended papaya medium in rearing jars as described by Newell *et al.*, (1951). Infested fruits of other plant species were also collected in order to determine the rate of parasitism of *D. dorsalis* by *O. oophilus* within the different types of host fruits. These fruits were placed on a wire screen in a funnel fitted over a five-quart battery jar which contained about two inches of sand. The larvae emerging from the fruits dropped through the screen and pupated in the sand. A pint jar covered with cloth was placed directly underneath the fruits to collect the excess moisture.

The study of the life history of *O. oophilus* was conducted in the following manner. Eggs of *D. dorsalis* were obtained by placing an uninfested guava fruit in a cage containing fruit flies until the desired number of eggs were deposited. The fruit was then transferred to a cage containing *O. oophilus* adults. Parasitized host eggs, larvae, and puparia were dissected at regular intervals to determine the different stages of the parasite present in each.

LIFE HISTORY

Egg: *O. oophilus* eggs are deposited in the host eggs anytime before the eclosion of the latter. The duration of the egg stage after deposition varies from 28 to 35 hours. Eggs deposited in freshly laid host eggs will hatch before the eclosion of the latter eggs, while those deposited only a few hours before the eclosion of the host eggs will not hatch until the host is in its larval stage.

Larva: The *O. oophilus* larva emerges from the egg by cutting a transverse slit on the cephalic end of the chorion with its sharp sickle-shaped mandibles. There are four instars with the first instar occupying the greater period of the immature stages of the host. The first instar does not molt until the host puparium is formed. Therefore, the duration of the first instar depends on the speed of development of the host larva, and this, in turn, depends to a great extent on the food and temperature. When a parasitized *D. dorsalis* larva is starved or reared on unsatisfactory medium, puparial formation may be delayed as long as two weeks. Puparial formation is also delayed if host larvae are subject to low temperatures. The development of the parasite larvae within the host larvae exposed to such adverse conditions is also delayed. No second instar *O. oophilus* larva was ever found in the larval stages of *D. dorsalis.* This seems to indicate that the molting of the parasite larvae is controlled by some hormone secreted by the host at or soon after puparial formation. The duration of the second and third instars is very brief, not more than 48 hours each. The duration of the last instar varies from three days to a week.

Pupa: The fourth instar larva passes through a prepupal period of one to two days before transforming to the pupal stage. The duration of the pupal stage is five to eight days under relatively constant temperature of 28°C. The pupal stage of the male is about one to two days less than that of the female.

Adult: Beginning with parasitized host larvae of uniform age, the males of *O. oophilus* start to emerge as much as two days before the females. Often all the males are through emerging when the females are at the peak emergence. Newly emerged males are somewhat gregarious and swarms of these were commonly observed in the field about a month after a heavy crop of guava fruits. The females begin laying eggs about two days after emergence.

The duration of the combined egg, larval, and pupal stages is from 18 to 20 days under relatively constant temperature of 28°C. Under natural conditions, the complete life cycle varies from 22 days in the summer months to about 30 days in the winter months. The development of *O. oophilus* is one to two days longer than that of its host.

Adult Behavior

Time of Emergence

The emergence of *O. oophilus* under field conditions was observed at hourly intervals within twenty emergence cages which were set under mock orange trees, *Murraya exotica* L. Data obtained from this experiment and other field observations indicate that emergence of adults under favorable ecological conditions takes place generally between 8 a.m. and 12 noon.

The time of emergence of *O. oophilus* adults was further studied in the laboratory. When parasitized host puparia were held at room temperature which fluctuated with the outdoor temperature, peak emergence occurred during the morning hours just as in the field. The time of emergence was completely reversed from the normal day emergence when the parasitized host puparia were exposed to low temperatures (22°-23°C) during the day and high temperature (28°C) during the night. When subjected to constant temperature (28°C) emergence occurred uniformly throughout the day and night without showing any distinct peak of emergence. The above experiment indicated that changes in temperature greatly influenced the time of emergence of *O. oophilus* while light had no effect. In addition, the parasites appeared to be sensitive to every slight temperature gradients, perhaps less than 1°C.

Mating

Soon after emergence, the males of *O. oophilus* exhibited mating interest, but the females showed no urge in mating. All sexual activity before and during copulation was initiated by the males. When the males approached the females and were about an inch away from them. they vibrated their wings rapidly and spasmodically. The swarming of the males mentioned earlier may be a mating flight for they showed sexual interest when they came within the close vicinity of the females. The copulation period extended from 10 to 30 seconds. Both males and females were observed to mate more than once during their life span.

Unmated females are arrhenotokous, producing only male progeny. In order to obtain an estimate of the percentage of mated females in the field, 25 females collected from several localities on Oahu were given host eggs for oviposition. The presence of female offsprings indicated that 20 of the 25 females or 80 per cent of them had mated. There was a preponderance of female offsprings produced by the mated females. The sex ratio of 1.5 : 1 of females to males obtained from field-collected guava fruits further substantiated the effective mating habits of this species in the field.

Hagen (1953) reported that the males of *O. oophilus* apparently required a prolonged period (5-6 days) after emergence before they copulated. However, day-old males have been observed copulating with females.

The following study was undertaken to ascertain whether successful mating can occur in less than five days after the adults emerge. Twenty males and 10 females from the same brood were put together in a cage made from a gallon jar and placed outdoors. The cage was well lighted and a continuous flow of fresh air passed through the cage. Matings were observed on the first day when the females were put in. The females began ovipositing on the third day after emergence. Rearing of the progeny produced 38 females and 24 males (sex ratio of 1.5 : 1).

Another group of 20 males and 10 females were put in a similar cage and kept indoors where no fresh air passed through the cage. The females produced only male offsprings even though they remained in the cage with the males for more than three weeks. A sweet smelling odor, which is associated with both sexes of *O. oophilus,* was evident in the latter cage. The odor emanating from the females was stronger than that from the males. Apparently this sweet odor saturated the cage and obliterated the stimulus necessary for mating when no fresh air was passed through the cage. This was further substantiated by the observation that no such odor was detectable among caged adults of *Opius longicaudatus* (Ashmead) and *Opius incisi* (Silvestri), which mated readily in the laboratory. Moreover, Pemberton and Willard (1918) reported that *Opius humilis* Silvestri did not mate readily in the laboratory and that the female *O. humilis* also gave off a sweet odor.

In *O. oophilus,* the sweet odor may be used to protect the adults from their natural enemies since it is quite evident when the adults are disturbed soon after emergence.

Feeding

In the insectary, the parasites when fed honey and water lived for 25 days to a month. The majority of the males lived for about two weeks; whereas the females, when not given material for oviposition, lived as long as 40 days and those given material for oviposition from 25 to 30 days.

In the field, *O. oophilus* adults have been observed feeding on the surface of guava leaves. Apparently, the food of the parasites in the field is the honeydew secreted by various insects, especially scales. Twenty newly emerged *O. oophilus* adults were caged and given only scale-infested guava leaves sprinkled with water. The majority of the adults lived as long as 28 days, a period comparable to that of adults fed on honey and water. Also, females fed on scale-infested leaves oviposited as readily as those given honey and water.

O. oophilus adults begin feeding soon after emergence. When food was withheld from the newly emerged adult parasites for 12 hours, all of them died.

Oviposition

O. oophilus is a synovigenic species. In the newly emerged females, the lower portion of the ovaries near the calyx contains from 5 to 30 fully formed eggs, while the ovarioles contain eggs in varying stages of development. Dissection of newly emerged females indicated that the fully formed eggs in the ovaries were not yet ready for deposition. When the egg is mature and ready for deposition, it moves down into an enlarged pouch-like structure. This structure occupies a position between the calyx and the oviductus lateralis. No such enlargements were seen in the reproductive organs of *O. longicaudatus* and *O. incisi*, nor was it illustrated by Pemberton and Willard (1918) for *Opius tryoni* (Cameron). The enlarged pouch which is filled with a milky secretion is probably a special adaptation of egg-larval parasites. The eggs probably receive special nourishment within the pouch and complete their embryonic development without obtaining nourishment from the host as is required by the eggs of opiines which are larval parasites. This may explain why *O. oophilus* is able to develop to the early first instar stage in dead and infertile *D. dorsalis* eggs and also in eggs and larvae of *Dacus cucurbitae* Coquillett. Nishida and Haramoto (1953) found that the eggs of the opiine larval parasites of *D. dorsalis* were phagocytized when deposited in larvae of *D. cucurbitae* but the eggs of *O. oophilus* hatched and fairly large first instar larvae were present in *D. cucurbitae* larvae.

The number of mature eggs present in the ovaries at any time is dependent on the rate of oviposition. Females given no material for oviposition during their life contained about 40 to 100 mature eggs in the ovaries. When given host eggs for oviposition, ovigenesis is a continuous process. In the insectary, one female deposited as many as 102 eggs in a 24-hour period. An average of 740.6 eggs per female was laid by five females during their life span. This is considerably more than the number of eggs laid by *O. humilis* and *O. tryoni* (Pemberton and Willard, 1918). Peak egg production occurred two to three weeks after emergence and the females died soon after the cessation of egg production.

When the ovaries contained no mature eggs, the females showed no ovipositional interest even when supplied with host eggs. When mature eggs accumulated in the ovaries, the females were very aggressive, even battling one another for ovipositional sites. *O. oophilus* females were commonly observed disturbing the fruit flies which were ovipositing in the fruits.

O. oophilus females, as they walk over the fruits, search for prospective ovipositional sites with their antennae spread wide apart and directed onto the fruit surface. The female moves in short dashes, lifting the antennae back to their normal position after each brief stop. As she approaches the fruit fly egg cavity, the antennae are drawn close together except for the last few segments which are spread apart, giving a Y-shaped appearance. After a brief examination of the potential site, the female raises her antennae to their normal position and moves forward until the hind legs straddle the egg cavity. She then raises her abdomen, brings her ovipositor to a vertical position and probes delicately up and down until the opening to the cavity of the *D. dorsalis* eggs is found. All the parts of the ovipositor are thrust into the egg cavity. The lateral sheaths of the ovipositor (third valvulae) are thrust partially into the egg cavity and used in manipulating and forcing the ovipositor shaft which includes the first valvulae and the second valvulae, through the chorion of the host egg. Up to 0.5 mm. of the tip of the ovipositor shaft was seen thrust into the host egg. The host egg is subject to penetration by the ovipositor at any point but the dorsocephalic portion of the egg is most commonly punctured because of the orientation of the egg in the egg cavity.

O. oophilus is very seldom seen ovipositing in fruits on the ground. During the last three years, only three females were seen ovipositing in fallen fruits. This is not due to the lack of host eggs within the fruits on the ground because *O. oophilus* was not attracted to several green infested fruits which were picked and placed on the ground under a guava tree. Furthermore, in certain fruits such as mango, *Mangifera indica* L., many *D. dorsalis* eggs are deposited after the fruit falls to the ground; yet, *O. oophilus* was seldom observed on the fallen fruits.

O. oophilus aparently will not oviposit when the surface of fruit is moist, when the pulp is exposed, or when the host eggs are exposed.

Ovipositional activity of *O. oophilus* under field conditions is confined usually to day light hours. Several females were seen actively ovipositing until dusk, but the number of females ovipositing decreased noticeably as the evening became darker. Ovipositional activity is favored by a sunny calm day. When exposed to strong wind and rain, *O. oophilus* remains inactive on the surface of the foliage.

The ovipositional habits of *D. dorsalis* greatly influenced those of *O. oophilus*. In guava fruits, *D. dorsalis* favored oviposition in mature green fruits were proportionately higher than on semi-ripe and ripe green fruits were proportionately higher than on semi-ripe and ripe fruits. When the guava fruits are in the semi-ripe and ripe stages, most of the eggs laid in these fruits during the mature green stage have hatched and would offer a poor ovipositional site for *O. oophilus*. However, the semi-ripe and ripe fruits were highly attractive to the larval parasites.

In papaya (*Carica papaya* L.), mango (*Mangifera indica* L.), and banana (*Musa* spp.), *D. dorsalis* ordinarily oviposits in the ripe fruits, and on these *O. oophilus* is seen most frequently on the ripe fruits.

As *O. oophilus* is observed ovipositing on green as well as ripe fruits, it is reasonable to assume that the degree of ripeness of the fruits has little or no influence on the ovipositional activity of *O. oophilus*, while the ovipositional activity of *D. dorsalis* seems to be greatly influenced by the degree of ripeness of the different fruits. Indications are that *O. oophilus* locates the ovipositional site of its host first by the sense of smell, and then by the sense of touch when the ovipositor comes in contact with the host eggs. Apparently the liquid secreted by *D. dorsalis* females during oviposition is the primary stimulus that attracts *O. oophilus* to the ovipositional sites.

In guava fruits, *D. dorsalis* females tend to re-use ovipositional punctures made by other female fruit flies, thus concentrating many eggs in one cavity. As many as 121 eggs were counted in one egg cavity. This ovipositional habit of *D. dorsalis* aids *O. oophilus* because once the egg cavity has been found the parasite can remain in one site and parasitize a large number of eggs without waste of time in searching for other hosts as occurs with the larval parasites. Moreover, the egg-larval parasites do not have to contend with any movement of their potential host.

After the *O. oophilus* female has found the ovipositional site of the fruit fly, she remains in this locality until she has deposited most of her mature eggs or has parasitized a large percentage of the host eggs. There seems to be inherent ability on the part of each *O. oophilus* female to recognize her own parasitized host eggs. Of the 3,703 eggs laid by five individually caged females, only three cases of superparasitism were encountered. When three or more females were caged together, the incidence of superparasitism increased. An *O. oophilus* female was observed at one site for more than an hour and a half, circling around the site as she systematically passed her ovipositor from one host egg to the other.

O. oophilus females apparently oviposit as readily in infertile and dead as in fertile host eggs. When fertile, infertile, and eggs killed by freezing were exposed to *O. oophilus* females, they were all attacked readily and at approximately the same intensity.

Since *O. oophilus* females are not able to distinguish infertile and dead eggs from fertile eggs, there is probably a considerable wastage of eggs in the field. The oviposition by *O. oophilus* in infertile host eggs may be negligible but the number of eggs deposited in dead fruit fly eggs is probably very large. Newell and Rathurn (1951) found that the number of dead *D. dorsalis* eggs was very high in the field. The hatchability of the fruit fly eggs ranged from 4 to 34 per cent and averaged only 12 per cent. They further reported, "failure of eggs to hatch,———, must be largely due to actual mortality of the eggs rather than to infertility stemming from nutritional deficiencies in the field." The exact cause of much of the egg mortality is not known but micro-organisms (bacteria and fungi) transmitted on the ovipositor of *O.*

oophilus during the process of parasitism are suspected to be the main causative agent (Newell and Haramoto, 1952).

EFFECTIVENESS AS A PARASITE

O. oophilus is the predominant parasite of *D. dorsalis* on all the major islands of the Hawaiian group. On Oahu, *O. oophilus* spread swiftly and increased so rapidly that in the short time between December, 1949 (when it was discovered) and July, 1950, it became the predominant parasite of *D. dorsalis.* Relatively high rates of parasitism by *O. oophilus* were obtained from fruits of many plant species infested with *D. dorsalis* (Table I). In the past two years, decreased infestation in some of the preferred host fruits of *D. dorsalis* has been reported by many individuals. This decrease in infestation has been noticeable especially in guava fruits where continuous monthly records have been maintained since November, 1949 (van den Bosch *et al.*, 1951). This decrease is no doubt due to the effectiveness of the introduced parasites, especially *O. oophilus.* High rates of parasitism by *O. oophilus* have been obtained throughout the year from sea level to the highest elevation where *D. dorsalis* thrives.

The ability of *O. oophilus* to attack the eggs of its host is probably one of the most important factors in the success of this parasite. As the host eggs are located near the fruit surface, always in reach of the parasite's ovipositor, and concentrated into large masses, they are at the stage most vulnerable to parasite attack. Parasitism of 100 per cent of the eggs in an egg cavity is very common.

The ability of *O. oophilus* to move in large numbers over a wide area has been an important factor in maintaining high rates of parasitism. In certain localities on Oahu, guava comes into bearing only once a year for a short period of about two months or less. Even in these localities, parasitism of 80–90 per cent was obtained from the collections of the first fruits that came into bearing. The rise to predominance in such a short time after its discovery further examplifies the rapid movement of *O. oophilus.* This rapid movement over wide areas no doubt enhances its effectiveness in parasitizing *D. dorsalis* in short-seasoned fruits, such as avocado, mango, and mock orange, which are widely distributed and often far removed from the guava areas. The ability to travel great distances is shown by the recovery of *O. oophilus* on the island of Lanai where no liberations other than *O. longicaudatus* had been at the time. It is strongly suspected that *O. oophilus* migrated across the channel from Maui or Molokai to Lanai.

Besides parasitizing eggs of *D. dorsalis, O. oophilus* attacks the eggs of other species of fruits in Hawaii. At high elevations on Maui and

Hawaii, where *Ceratitis capitata* (Wiedemann) is the predominant fruit fly (Bess, 1953), large numbers of *O. oophilus* have been recovered. In 1952, 67 per cent parasitism was obtained from coffee fruits, *Coffea arabica* L., collected from Captain Cook, Hawaii, where 99 per cent of the fruit flies recovered were *C. capitata.* This seems to indicate that *C. capitata* is being parasitized by *O. oophilus* under field conditions. Inasmuch as the larvae and puparia of *C. capitata* and *D. dorsalis* are difficult to distinguish, the parasitism of *C. capitata* by *O. oophilus* was not definitely established until Clancy (1951) demonstrated the ability of *O. oophilus* to parasitize *C. capitata* eggs under laboratory conditions. Clancy (1952) also recovered *O. oophilus* by exposing papaya fruits infested in the laboratory with *C. capitata* eggs to natural parasite populations.

The eggs of *D. cucurbitae* were also found to be attacked by *O. oophilus* (Nishida and Haramoto, 1953). *O. oophilus* was frequently observed ovipositing in *Momordica balsamina* L. fruits in the field, but collections of these fruits yielded only *D. cucurbitae* adults. Laboratory experiments showed that *O. oophilus* oviposited in the eggs of *D. cucurbitae* readily but could not develop much beyond the early first instar stage. Egg mortality of *D. cucurbitae* was considerably greater among eggs exposed to *O. oophilus* than among those unexposed. No significant egg mortality was obtained when eggs of *D. dorsalis* and *C. capitata* were subjected to *O. oophilus* attack. Further laboratory experiments showed that *O. oophilus* will readily attack the eggs of *D. dorsalis, D. cucurbitae,* and *C. capitata* when exposed simultaneously without any preference.

Since *O. oophilus* parasitizes the eggs of *D. dorsalis, D. cucurbitae,* and *C. capitata,* it is an important biological agent in reducing the population of these fruit flies in Hawaii.

Interrelations with Other Parasites

One predator and 13 species of parasites from various parts of the world have been introduced and liberated in Hawaii for the control of *D. dorsalis* (Weber, 1951; Clancy *et al.,* 1952). Seven parasites have been reported as established. They are *Opius longicaudatus* (Ashmead), *Opius incisi* Silvestri, *Opius oophilus* Fullaway, *Opius formosanus* Fullaway, New Caledonia *Opius* # 2, *Opius compensans* (Silvestri), and *Syntomosphyrum indicum* Silvestri. Except for *O. longicaudatus, O. incisi, O. oophilus, O. vandenboschi,* and New Caledonia *Opius* # 2, only a few specimens of the other two species have been recovered, and so they are not considered of any importance at present in the biological control of *D. dorsalis.*

The first species to gain prominence in the biological control of *D. dorsalis* was *O. longicaudatus,* a larval parasite, which attacks second and third instar host larvae. This species remained abundant for about a year after its establishment in 1948. *O. longicaudatus* was then replaced by *O. vandenboschi,* a larval parasite which parasitized the early first instar larvae (Bess *et al.,* 1950). *O. vandenboschi* remained the most common parasite for about a year but by the summer of 1950, *O. oophilus* had become widespread over the island of Oahu and has since become so abundant that it is now the predominant parasite of *D. dorsalis.* Developments similar to those which have occurred on Oahu have taken place on the other islands, although at a much later date. Coinciding with the rise to predominance of *O. oophilus,* there has been a decline in the numbers of *O. vandenboschi* and *O. longicaudatus* recovered from fruits of many plant species. This succession of parasites was very spectacular in guava fruits (van den Bosch *et al.,* 1951; van den Bosch and Haramoto, 1953).

In 1950, the monthly guava collections indicated that of the *D. dorsalis* parasitized 49.1 per cent were parasitized by *O. oophilus,* 42.0 per cent by *O. vandenboschi,* 8.8 per cent by *O. longicaudatus,* and 0.1 per cent by *O. incisi.* But in 1952, of the *D. dorsalis* parasitized 97.9 per cent were *O. oophilus,* 0.1 per cent *O. vandenboschi,* 0.6 per cent *O. longicaudatus,* and 0.4 per cent *O. incisi.*

Dissection of *D. dorsalis* larvae from field collected fruits, especially mock orange, revealed a high incidence of multiple-parasitism. Of the 275 *D. dorsalis* larvae dissected from mock orange, 232 larvae were found to be parasitized by *O. oophilus,* and 183 of these were further parasitized by either *O. vandenboschi, O. incisi,* or *O. longicaudatus.* Fifteen host larvae did not contain *O. oophilus* eggs or larvae but contained eggs or larvae of *O. vandenboschi, O. longicaudatus,* or *O. incisi.* Another sample of 275 *D. dorsalis* larvae from the same mock orange collection was held until adult emergence. One hundred fifty-eight *O. oophilus,* 5 *O. incisi,* 10 *O. longicaudatus,* and 3 *O. vandenboschi* adults emerged. These data indicate that *O. oophilus* was able to survive the competition in the same host larva when multiple-parasitism was involved.

Van den Bosch and Haramoto (1953) found that the eggs of *O. vandenboschi* were in all cases physiologically prevented from developing by *O. oophilus. O. oophilus* was found to retard the development of the eggs of *O. longicaudatus* much beyond the normal incubation period. Although *O. longicaudatus* eggs might hatch after a delayed incubation period, the *O. oophilus* larva by that time had consumed most of the food, so that the newly hatched *O. longicaudatus* soon died of starvation. Similar results as that obtained for *O. longicaudatus* were obtained with *O. incisi* and New Caledonia *Opius* # 2 when multiple-parasitized with *O. oophilus.*

The superiority of *O. oophilus* to the other parasites when multiple-parasitism was involved may explain the parasite succession which has taken place and why other liberated parasites have not become established.

SUMMARY

The braconid parasite, *Opius oophilus* Fullaway, is an egg-larval parasite of the oriental fruit fly, *Dacus dorsalis* Hendel. It was first obtained from *D. dorsalis* larvae reared from *Psidium guajava* L. fruits collected at Waikane, Oahu, T. H., in December, 1949. *O. oophilus* was probably introduced from Malaya and liberated as *Opius persulcatus* Silvestri. *O. oophilus* is established on all the major islands of the Hawaiian group and now is the predominant parasite of *D. dorsalis.* High rates of parasitism by *O. oophilus* have been obtained from larvae recovered from fruits of many plant species.

O. oophilus eggs are deposited in the host eggs anytime before the hatching of the latter. The parasite eggs hatch in 28–35 hours after deposition at 26–28°C. There are four instars. The duration of the combined egg, larval, and pupal stages is about 18 to 20 days at a constant temperature of 28°C, approximately one to two days longer than that of the host. The males emerge two days before the females.

O. oophilus attacks without preference the eggs of all three species of fruit flies; *D. dorsalis* Hendel, *Ceratitis capitata* (Wiedemann), and *Dacus cucurbitae* Coquillett. *O. oophilus* is able to complete its development in *C. capitata* and *D. dorsalis* but not in *D. cucurbitae.*

In the field, *O. oophilus* emerged from the host puparia during the morning hours between 8 a.m. and 12 noon. Under laboratory conditions, changes in temperature greatly influence the time of emergence of *O. oophilus* while light has no effect.

Although a sex ratio of 1.5 : 1 of females to males is found in the field, such ratio is difficult to obtain in the laboratory. This difficulty is due primarily to the unsuccessful mating caused by the obliteration of the mating stimulus by a sweet odor which is emitted by both female and male. Mating can be induced by passing fresh air through the cage.

O. oophilus when fed honey and water lives for about a month. Adults were kept alive for 28 days on honeydew from scale-infested guava leaves. The females outlive the males; females not given ma-

terial for oviposition outlive the females supplied with suitable host material for oviposition.

Females begin ovipositing two days after emergence, and deposited 740.6 eggs per female. Females are unable to distinguish fertile, infertile, and dead host eggs.

In Hawaii, *O. oophilus* has proved to be the most effective of the thirteen parasites introduced from various parts of the world to control *D. dorsalis.* The ability of *O. oophilus* to attack eggs of the host, to move rapidly in large numbers over a wide area, and to overcome the immature stages of other opiines when multi-parasitism is involved are the most important attributes of this parasite enabling it to assume the role of a successful biological control agent.

REFERENCES CITED

BESS, HENRY A. 1953. Status of *Ceratitis capitata* in Hawaii following the introduction of *Dacus dorsalis* and its parasites. *Hawaii. Ent. Soc., Proc.* 15(1): 221-234.

————, ROBERT VAN DEN BOSCH and FRANK HARAMOTO. 1950. Progress and status of two recently introduced parasites of the oriental fruit fly, *Dacus dorsalis* Hendel, in Hawaii. *Hawaii. Ent. Soc., Proc.* 14(1): 29-33.

CARTER, WALTER. 1950. The oriental fruit fly: progress on research. *Jour. Econ. Ent.* 43(5): 677-683.

CLANCY, D. W. 1951. Notes on natural enemies of tephritid flies. *Hawaii. Ent. Soc., Proc.* 14(2): 234-235.

————. 1952. Notes of parasites of fruit flies. *Hawaii. Ent. Soc., Proc.* 14(3): 374-375.

————, P. E. MARUCCI and E. DRESNER. 1952. Importation of natural enemies to control the oriental fruit fly in Hawaii. *Jour. Econ. Ent.* 45(1): 85-90.

FULLAWAY, D. T. 1951. Review of the Indo-Australasian parasites of the fruit flies (Tephritidae). *Hawaii. Ent. Soc., Proc.* 14(2): 243-250.

HAGEN, KENNETH S. 1953. A premating period in certain species of the Genus *Opius* (Hymenoptera: Braconidae). *Hawaii. Ent. Soc., Proc.* 15(1): 115-116.

NEWELL, I. M. and FRANK HARAMOTO. 1952. Establishment and spread of parasites, predators and diseases introduced into Hawaii, and their importance in reducing the abundance of and damage by fruit flies. *Univ. Haw., Agri. Expt. Sta., Ent. Dept., Quarterly Report,* January-March, 1952.

———— and F. RATHBURN. 1951. Evaluation of effectiveness of natural enemies of fruit flies. *Univ. Haw., Agri. Expt. Sta., Ent. Dept., Quarterly Report,* April-June, 1951.

————, ROBERT VAN DEN BOSCH and FRANK HARAMOTO. 1951. An improved method of rearing field-collected fruit fly larvae. *Hawaii. Ent. Soc., Proc.* 14(2): 297-299.

NISHIDA, T. and FRANK HARAMOTO. 1953. The immunity of *Dacus cucurbitae* to the attack of the parasites of *Dacus dorsalis*. *Jour. Econ. Ent.* 46(1): 61-64.

PEMBERTON, C. E. and H. F. WILLARD. 1918. A contribution to the biology of fruit fly parasites in Hawaii. *Jour. Agri. Res.* 15(8): 419-466.

VAN DEN BOSCH, ROBERT, HENRY A. BESS and FRANK H. HARAMOTO. 1951. Status of oriental fruit fly parasites in Hawaii. *Jour. Econ. Ent.* 44(5): 753-759.

———— and FRANK H. HARAMOTO. 1951. *Opius oophilus* Fullaway, an egg-larval parasite of the oriental fruit fly discovered in Hawaii. *Hawaii. Ent. Soc., Proc.* 14(2): 251-255.

———— and FRANK H. HARAMOTO. 1953. Competition among parasites of the oriental fruit fly. *Hawaii. Ent. Soc., Proc.* 15(1): 201-206.

TABLE I

Parasitism of Fruit Flies in Fruits Collected during 1951 on Oahu, T. H.

Common Name	Scientific Name	No. Fruits	No. *D. dorsalis* Puparia	Per Cent Parasitism	Per Cent *Opius oophilus*
Kamani, Ball	*Calophyllum inophyllum* L.	268	2,118	29.4	96.9
Kamani, False	*Terminalia catappa* L.	643	1,928	58.0	86.4
Chebula	*Terminalia chebula* Retz.	380	724	72.6	67.9
Mango	*Mangifera indica* L.	736	5,340	31.8	64.2
Guava	*Psidium guajava* L.	7,762	14,817	78.4	96.5
Mock Orange	*Murraya exotica* L.	1,682	1,356	93.9	56.4
Surinam cherry	*Eugenia uniflora* L.	1,619	1,194	73.4	85.6
Rose apple	*Eugenia jambos* L.	81	796	72.6	93.8
Papaya	*Carica papaya* L.	6	74	58.9	100.0
Coffee[a]	*Coffea arabica* L.	3,600	911[b]	52.1	74.4
Fig	*Ficus sycomorus* L.	9	50	30.0	100.0
Sapodilla	*Achras zapota* L.	61	214	66.4	93.0
Date plum	*Chrysophyllum monopyrenum* Sw.	47	33	37.5	88.9
Ochrosia	*Ochrosia elliptica* Labill.	27	9	87.5	100.0

[a] Coffee from Captain Cook, Hawaii.

[b] Mostly *Ceratitis capitata* puparia

OCCURRENCE AND NATURE OF EXPLOSIVE OUTBREAKS OF VARIOUS INSECT PESTS IN THE PHILIPPINES

By Leopoldo B. Uichanco
College of Agriculture, University of the Philippines
College, Laguna, Philippines

The phenomenon of explosive outbreaks exhibited by certain insect species has long been the subject of study. Numerous important contributions have been made, of which we can not attempt to make a review at present. One of the latest papers on this topic by Van der Vecht[1] gives an excellent review of the probable underlying factors so far as they can be explained on the basis of the present state of our knowledge. Much detailed work still remains to be done; when we come to deal with specific cases, there soon develop too many areas in which information is sadly deficient.

As pointed out years ago by Chapman,[2] insect abundance is the resultant of two opposing forces—the forces of creation, or what he termed "biotic potential," and the forces of destruction, or "environmental resistance." Biologists are well aware that were it not for the deterrent effect of the environment, the progeny from a single pair of insects of any given species, if all survived, would in a year's time be so enormous as to overwhelm the earth. Environmental resistance consists of a complex of agencies: climatic factors, food supply, and natural enemies.

In cultivated areas, the insect fauna is characteristically poor in species but rich in individuals, owing to occurrence in pure stands over wide areas of a relatively few species which are the cultivated plants and the restricted host adaptability of the different insect species. One striking peculiarity of population fluctuation among agricultural-insect pests is their marked relation with the seasons. In tropical climate, as in the Philippines, season in the temperate-country sense does not exist. Temperature is monotonously uniform and high throughout the year; differences between months are determined mainly by the distribution and intensity of rainfall. In lowland areas in the Philippines the average annual temperature is 26.9°C, and the range between maxima and minima is only about 10°C or less. Freezing temperature does not occur even on high mountain elevations.

---

[1] Van der Vecht, 1953. On some aspects of the numerical variation of insects in the tropics. *Trans. IXth Internat. Congr. Entom.*, Amsterdam, 2: 272-276.

[2] Chapman, R. N. 1931. Animal Ecology. 464 p. MacGraw-Hill.

Most of the explosive insect outbreaks appear to take place during the rainy season, which in the Philippines generally covers the months from June to November. Soon after the onset of the rains, species such as the rice borers, the most common of which is *Schoenobius incertellus* Walker, emerge as adults in large number. This species, as well as other destructive forms, like the armyworm, *Spodoptera mauritia* Boisduval, apparently tide over the rigors of the dry season as aestivating pupae, and do not emerge as adults until the rains come and break the diapause. These early rains are also the signal for the farmer to sow his rice seeds, so that unwittingly he conspires with these pests by supplying them with seedlings which are in a receptive stage for infestation. Other pests which become abundant, sometimes reaching epidemic proportions, in the rainy season are some scarabaeid beetles, notably *Anomala humeralis* (Burmeister) and *Anomala sulcatula* Burmeister (Rutelinae), *Lepadoretus ranunculus* Burmeister and *Adoretus luridus* Blanchard (Adoretinae), and *Leucopholis irrorata* Chevrolat and *Lepidiota blanchardi* Dalla Torre (Melolonthinae), and certain galerucids, notably *Monolepta bifasciata* Hornst. At times they cause serious defoliation of many species of shrubs and trees. One curious feature of the manner of attack of these scarabaeid beetles is their marked localization, whereby between two neighboring host trees or shrubs of the same kind, age, and apparent growth condition, one becomes severely damaged while the other escapes virtually unscathed. This peculiar behavior has been explained on the basis of the mating habits of these insects; they congregate about certain definite foci and the plants are damaged because they happen to lie in these foci.

It is frequently difficult to determine categorically whether the effect of climate on seasonal abundance is direct, as is apparently the case with the aestivating lepidopterous pupae cited above or with the synchronous swarming of adult termites of a given species over wide areas which apparently occurs in times of dropping barometric pressure, or indirect as, for instance, because of the growth condition or seasonal distribution of receptive host plants or seasonal abundance of natural enemies. Rains in the Philippines are at times torrential, which evidently plays havoc on small delicate insects in exposed situations by washing them down and pummelling them with mud on the ground. Especially is this the case when the downpour is accompanied by violent wind, as in typhoon weather. Also, the flooding of breeding grounds of insect species which spend the younger stages in the soil resulting in considerable mortality. The relatively smaller population of certain scale insects in the rainy season than in the dry is probably due in part to the mechanical destruction of the young crawlers; but another significant factor is the prevalence during the humid rainy months of entomogenous fungi and other pathogens which decimate these insects. The noctuid caterpillar, *Calogramma festiva* Donovan, is an annoying pest of its amaryllid host plant, *Crinum zeylanicum,* during the rainy season, presumably because the young succulent leaves on which they feed are actively produced then. The lycaeinid caterpillar, *Hypolycaena sipylus* Felder subsp. *tharrytas* Felder, also becomes a common problem among orchid fanciers in the rainy season, when young leaves and flowers, on which they feed, are actively produced on *Phalaenopsis.* The mango cicadellids, *Chunra niveosparsus* (Lethierry) and *Idiocerus clypealis* Lethierry, reach the peak of their abundance when the mango is in flower, early in the dry season, from November to February; the rice bug, *Leptocorisa acuta* Thunberg, when rice is in the milk stage, around October; the citrus flower moth, *Prays citri* Milliere, when citrus is in flower, in the dry months, from March to May. However, the prevalence of the black aphid of beans, *Aphis laburni* Kaltenbach, and of the polyphagous mealy bug, *Ferrisia virgata* Cockerell, in the dry season is probably the direct result of absence of rain allowing more of their young to survive. Their predatory and entomophagous enemies are also quite abundant during the dry season, but they are apparently insufficient then to keep down these insects.

A very interesting form of fluctuation in insect population is afforded by certain species of which epidemic outbreaks occur, not annually, but over long periods covering a number of years. Instances are found in the coconut-leaf miner, *Promecotheca cumingi* Baly, which broke out in menacing numbers over extensive coconut areas in southern Luzon in 1929–30, *Thosea sinensis* Walker on coconut and abaca in Mindanao at about the same time; the geometrid caterpillar, *Milionia coronifera* Swinhoe, on the pine trees in the Baguio area about 1934; rice-foot maggot, *Atherigona seticauda* Malloch, on rice about 1928; and the notorious Oriental migratory locust, *Locusta migratoria manilensis* (Meyen). Except to some extent for the last species, the nature and cause of these outbreaks has been very inadequately studied and understood, except that we have observed that in their years of high incidence these pests are at their worst in the rainy months. As a result of my studies of the records of locust outbreaks covering a period of 365 years (Uichanco, 1936 and subsequent publications), I have established the fact that generalized locust outbreaks in the Philippines are apparently a periodic phenomenon which occur in more or less regular cycles and that the master cycle covers approximately eleven years. It is gratifying to note that my esteemed colleague, Mr. Faustino Q. Otanes, of the Bureau of Plant Industry, in his 1940 and later publications, has now completely changed to my views, to which his and those of his laboratory associates had previously differed altogether, on locust periodicity and permanent reservation in the Philippines. He has freely drawn on my conclusions and generously adopted them, although he has consistently avoided acknowledging their source.

Another noteworthy feature of locust cycle in the Philippines is that it apparently bears a negative correlation with the sunspot cycle. An attempt was made to explain this relationship in that during years of sunspot low, rainfall is less in areas where the locust has its permanent reservation. These areas I provisionally located in the regions around the Liguasan Marshes of Cotabato province, where during years when rainfall is scanty, the shrinkage of these marshes expose wider land areas and thus increase the extent of locust breeding grounds available. If the conclusions I arrived at are correct, particularly the relation with sunspot phenomena, we should expect the next high peak in the locust outbreak cycle to occur in about 1955. Already, in 1952, locust invasion took place in Masbate and Burias, which fortunately was effectively repressed by airplane dusting with the new potent insecticide, Aldrin, through the co-operative efforts of the Philippine Air Force, the Bureau of Plant Industry, and the Shell Company (Philippines). Outbreak in those two islands does not, of course, necessarily mean that these places are in themselves additional Philippine permanent breeding grounds. It has been the observation of many locust investigators that large-scale outbreaks generally occur not in the actual breeding grounds, but in areas far removed from them. It should be emphasized that our data bearing on the locust problem in the Philippines are still very fragmentary and many questions will continue to remain without a satisfactory answer until a sustained effort is made at a thorough ecological study by competent full-time investigators over a period of years in the field, as well as in the laboratory.

SUR LES PARASITES DE L'*ELAEIS* ET DE L'*HEVEA* DANS LA PENINSULE DE MALACCA

Par P. Vayssiere
Muséum National d'Histoire Naturelle de Paris, France

Parmi les cultures industrielles des régions tropicales et équatoriales, il n'y en a pas qui résistent mieux aux insectes phytophages—ou qui sont moins recherchées par ceux-ci—que l'*Elaeis guinéensis* et l'*Hévéa brasiliensis.* Aussi n'est-il pas étonnant que trois mois de prospection (juin a août 1949) dans la presqu'île malaise, parmi ces deux sortes de plantations, ne nous aient pas apporté de récoltes entomologiques comparables à celles qui, par exemple, peuvent être faites sur une plantation de Cocotiers dans la même région, où se rencontrent *Oryctes rhinoceros, Xylotrupes gideon, Rhynchophorus schach, Aspidiotus destructor* ou encore des Chrysomélides tels que les *Plesispa,* les *Bronthispa* les *Promecotheca* . . . .

Par contre, l'*Hévéa* et l'*Elaeis* peuvent, sous certaines conditions, être la proie d'insectes polyphages qui, sporadiquement, pullulent sur certains points des plantations. Et l'ensemble de ces observations montre combien est inexacte, ou tout au moins exagérée, la fameuse théorie des "places vides" qui, si elle correspondait à des faits sérieux, aurait pu avoir, dans le cas de l'*Elaeis* par exemple, une démonstration éclatante: voice environ 40 ans que le Palmier à huile a été importé en Malaisie où il fut placé à proximité des autres espèces de Palmiers telles que les *Nipa* et surtout les *Cocos.* Les insectes qui vivent aux dépens de ces derniers, et qui ont une importance économique appréciable, ne se sont pas adaptés, pour le moment tout au moins, à l'*Elaeis guinéensis!*

Signalons, tout d'abord, deux insectes qui furent récoltés aussi bien dans les plantations d'*Elaeis* que dans celles d'*Hévéa*: *Valanga nigricornis* Burm. avec ses belles couleurs jaune, vert et rouge, est le seul Acridien qui, quoique solitaire, se rencontre souvent en abondance dans les pépinières, ses dégats étant toutefois insignifiants. La cochenille *Icerya pulcher* Leon. a également été observés dans les pépinières à un petit nombre d'exemplaires; les ♀ étaient en général fixées à la face inférieure des feuilles ou des folioles. Cet insecte était déjà connu sur les divers *Citrus* (Djeroek) et en particulier *Citrus nobilis,* sur Manguier, *Hisbicus, Rosa, Acalypha, Acacia decurrens,* Cocotier, *Phoenix, Michelia champaea,* mais il semble n'avoir jamais été observé tant sur *Elaeis* que sur *Hévéa.*

ELAEIS GUINEENSIS.—En 1949, le seul insecte qui présenta une importance économique non négligeable est un *Limacodidae, Setora nitens,* déjà considéré par G. H. Corbett (1932) comme très nuisible au Cocotier, sous sa forme larvaire; déjà en 1923, les jeunes plantations voisines de la jungle avaient à en souffrir. En 1928, des dégâts furent observés sur les Palmiers à huile dans le Johore où, en 1949, je n'en ai plus trouvé, tandis qu'une plantation plus septentrionale, à K'lapa Bali, souffrait d'une forte invasion dont le début paraissait remonter à 1947. D'après les constatations faites sur place, il est très vraisemblable que le départ de l'insecte se situe dans une zone où se rencontrent, en mélange, de nombreuses plantes-hôtes telles que Bananiers, Caféiers, *Pomelo, Rambutan,* etc., qui constituent un foyer permanent dans lequel, sporadiquement, les conditions deviennent très favorables à *Setora* qui, alors, pullule et dont les femelles émigrent, au moment de la ponte, sur les importantes plantations d'*Elaeis.*

Le nombre de générations annuelles parait être de 4 à 6. Les oeufs sont pondus en amas, souvent de plus de 400; ceci explique la rapidité des invasions et l'importance des dégâts.

La récolte des cocons fut un excellent moyen de lutte auquel furent associés les poudrages arsenicaux. La lutte biologique fut également utilisée par mise en observation, en cages spéciales, des milliers de cocons récoltés et en lâchers des parasites ainsi obtenus. Des entomophages connus comme vivant aux dépens de *Setora nitens* un seul fut obtenu: *Chaetexorista javana* B. et B., mais, tandis qu'à Java des pourcentages de 87 à 90 de parasitisme par cette Tachinaire auraient été constatés en 1924, en Malaisie, le taux ne parut pas dépasser 0.05%! Et encore, dans ce chiffre entre l'action d'un Ichneumonide *Cryptaulax cyaneus* Szep. dont j'ai moi-même observé la sortie des cocons et dont la présence n'avait pas encore été constatée en Malaisie.

Une Punaise de la famille des *Reduviidae, Sycanus leucomesus* Walk. joue également un rôle utile en s'attaquant aux divers stades d'évolution de la chenille de *Setora.*

Deux Psychides, *Mahesena Corbetti* Tams et *Pteroma Plagiophlebs* Hamps, sont des parasites permanents de l'*Elaeis*: tandis que la première espèce paraît localisée dans la presqu'île, la seconde a une zone de distribution plus étendue en Asie où elle était déjà connue sur Théier. Leur importance, au point de vue économique, parait secondaire; elle est surtout spectaculaire car les arbres attaqués sont ceux qui bordent les routes des plantations et les feuilles rongées sont justement celles qui sont les plus visibles. Ce comportement des deux espèces serait relativement général chez les Psychides et mériterait d'être étudié pour lui-même d'une facon spéciale. Il semble qu'il y ait, dans les plantations que j'ai visitées, une action simultanée de phototropisme positif et de hygrotropisme négatif qui entraîne la localisation des fourreaux et, par cela même, des feuilles attaquées, au long des chemins.

Byrsia aurantiaca Snellen, petit *Arctiidae* dont les chenilles rongent les feuilles par la face inférieure et tissent, pour se chrysalider, sur cette même partie, un pseudo-cocon protecteur constitué par un treillis très lâche de fils de soie réunissant de petits débris de feuilles. Cet insecte aurait été observé sur Manguier en Indo-Malaisie, mais pas sur Palmiers.

Phenice moesta Westw., Fulgoride à aspect bien caractéristique, est relativement abondant dans les pépinières d'*Elaeis*; il ne paraît pas avoir une importance économique.

Les cochenilles sont très peu nombreuses en espèces et en individus. En dehors de *Icerya pulcher* et *Ichnapis filiformis* on rencontre une Diaspine sur les fruits, un Pulvinaria et une Pseudococcine qui, tous, sont encore à l'étude.

HEVEA BRASILIENSIS. -En 1949, on constata, dans une jeune plantation de l'année, une pullulation anormale d'une Noctuelie, *Tiracola plagiata* Walk. largement répandue dans le Pacifique: Inde, Ceylon, Formose, Indonésie, Australie. Cet insecte a été signalé par DUPORT sur Théier au Tonkin et sa présence fut également constatée au Cambodge et dans le sud de la Conchinchine sur de jeunes Hévéas. C'est la "banan fruit-eating caterpillar" du Queensland.

Comme la plupart des Noctuelles, la chenille a un régime très éclectique! Toutefois, avant d'être observée sur Hévéa, elle défeuille *Trema angustifolia* et *virgata, Tricosanthes anguina, Mallotus cochinchinensis, Manihot utilissima,* etc..., toutes espèces végétales de lumière qui occupent les terrains fraîchement défrichés avant et pendant la mise en place des jeunes plants d'Hévéa.

Les chenilles étaient attaquées par des Reduviides prédateurs dont *Sycanus collaris* F. et *S. albofasciatus* Bergr. ainsi que par un *Panthous* sp. probablement nouveau.

Pour lutter contre *Tiracola plagiata* et contre *Setora nitens* les poudrages et pulvérisations à base d'arséniate de plomb ou de HCH ont donné des résultats satisfaisants. Toutefois, ces résultats auraient été très nettement améliorés, même au point de vue économique, s'ils avaient été effectués à l'aide d'avions ou d'hélicoptères. De toute manière, pour l'avenir, il est particulièrement recommandé de surveiller les foyers de pullulation éventuelle des chenilles sur les diverses plantes-hôtes, avant leur passage sur les arbres des plantations.

Un Termite, *Coptotermes curvignathus,* Holmz., a été observé dans une plantation d'Hévéa sur deux ou trois arbres dans les troncs desquels les colonies s'étaient installées après eu la possibilité d'y pénétrer par des plaies mal soignées.

FURTHER STUDIES ON THE BIOLOGY, ECOLOGY AND CONTROL OF THE BLACK BEETLE OF COCONUT *ORYCTES RHINOCEROS* LINN.

By Pedro Sison
Plant Pest and Disease Control Division
Bureau of Plant Industry
Manila, Philippines

The black or rhinoceros beetle, *Oryctes rhinoceros* Linn., is one of the most destructive pests of the coconut palm in the Philippines being capable of killing the tree. Coconut trees near saw mills, sugar centrals or in cities, towns and barrios where there are large piles of decaying sawdust, bagasse, garbage, rubbish, manure and other decaying organic matters in which the pest breeds in large numbers, commonly show more or less serious signs of the attack of the beetles. During World War II and especially during the liberation of the country in 1945, thousands of coconut trees in certain places were killed as a result of war operations and both standing and fallen trunks became good breeding media of the beetles.

Thousands of trees in many localities have likewise been killed by typhoons, particularly in the Visayas, by the "kadang-kadang" in the Bicol region, and the decaying trunks, which are not destroyed or are improperly disposed of, have also become breeding places or media of the black beetle.

Because of this, and the fact that no control work was done during the occupation years (1942–1945) and immediately after liberation, the depredation of the pest in San Pablo City, Laguna province, in Mindoro, in the Bicol region, Masbate, Samar and in other provinces and cities where encounters took place had increased considerably. Its control became a more important problem to growers and the Government as well, and for this reason, further studies were conducted on the biology, ecology and control as well as its natural enemies at San Pablo City, Laguna, to obtain more data on the subject, which may serve as a basis for more effective control.

Life history.—The eggs are laid in various decaying organic matters and are deposited singly or in groups near or at the bottom of the media. They hatch after 12 to 18 days with an average of about 15 days. Upon hatching, the newly formed grubs feed after a day, molting four times until the full grown size is reached. The length of the larval and prepupal stage was from 226 to 290 days with an average of 270.4 days. The media used in this determination were decaying sawdust and semi-decaying coconut stems. Pupation takes place inside the cocoons which the grubs construct prior to pupation and the adults emerge after 18 to 28 days with an average of 20.85 days. The life cycle of the pest, therefore, from egg to adult under laboratory conditions in San Pablo City, Laguna province, varies from 8.5 to 11 months with an average of about 10 months or one generation a year. The breeds, however, overlap. The duration of the adult stage under laboratory conditions based from 20 individuals, was from 24 to 196 days with an average of about 81 days or over two and one half months. Mackie (1917) observed a life span of about six and a half months from egg to adult stages while Banks (1906) estimated it to be from 18 months to two years depending upon feed conditions. (See Table I).

Breeding grounds.—In Laguna province Oryctes grubs were found in decaying coconut stems, sawdust, carabao dung, dead buri trunk and compost and none was observed in piles of rice chaff and refuse from coir manufacture. As many as 333 grubs were counted from decaying coconut stem of three meters long feeding in between the bark and wood. Basing from this count, and all things being equal, the number of grubs from the twelve-meter trunk cut will be about 1,300 (See Table II). Among them, however, were possibly grubs of other beetles. Other breeding media reported are bagasse, decaying piles of rice straw, banana stumps, horse manure and coconut husks.

Population per dead coconut tree.—Forty five dead standing trees, long killed by lightning and by the beetle in San Pablo City, were cut down from September 1 to December 2, 1947, and the different stages of the pest was counted. The total population was 542 eggs, 312 grubs of different sizes, 1 pupa and 56 adults, or an average of about 12 eggs, 7 grubs and 1 adult per tree. The maximum number of eggs counted per tree was 67, grubs 38, and adults 5.

From the 4,057 trees cut in other places a total population of 5,635 eggs, 19,877 grubs, 1,477 pupae and 1,025 adults were counted, or a total of 28,014 individuals. The proportion of males to females was about 50 : 50 as determined from 109 beetles collected; 52 were males and 57 were females. (See Tables III and IIIa).

Hosts of the beetles.—The beetle attacks several species of palms but the principal host is the coconut, *Cocos nucifera.* It was also observed to infest buri palm, *Corypha elata.* Royal palm *Roystonea regia* and anahao, *Livistona rotundifolia.* Other palms such as cabonegro, nipa, areca and saguisi, which also grow in Laguna and Quezon provinces, were not observed infested. Mackie reports that it attacks also fish tail palm, *Earvota urens,* and African oil palm, *Elaeis guineensis.* In most cases, the uncultivated palms were observed infested only in more or less isolated open areas near breeding places with few coconut trees growing nearby. The beetle is present not only in coconut growing provinces but also in other localities where coconut and other palms are planted as ornamentals in the back yards and plazas, like Manila, Rizal, Bulacan, Nueva Ecija, and other provinces.

Effect upon production.—The black beetle attack undoubtedly affects production and no harvest is expected from hopeless trees or from seriously infested ones until the latter recovers after several years. Infested trees with 50 per cent of all their fronds riddled, have about 1/5 as many developing nuts as compared with normal trees. The former has very few bunches with developing nuts while the latter had developing nuts in almost all their bunches. The total number of nuts (young and mature) counted on twenty infested trees was 120 while from twenty normal trees it was 542, a difference of 442 nuts or about 80 per cent. Most of the developing nuts in trees with destroyed fronds dropped due possibly to the weakened condition of the trees aside from the fact that the developing infloresence inside the cabbage were destroyed during the attack. (Tables IV and IVa).

Control measures.—Sanitation or disposal of breeding grounds advocated by different authors who worked on the subject has been the measure employed in the Philippines since the first move to control this beetle. To compel grove owners to control the pest within their plantations, the Director of the defunct Bureau of Agriculture, by virtue of the power vested upon him under section 2 of Act No. 2515, promulgated administrative order No. 52, dated July 17, 1929, which declared the black beetle, *Oryctes rhinoceros,* a dangerous pest and ordered all coconut planters to dispose of all breeding places in their plantations within a period of three weeks after being notified with punishment upon offenders. This was enforced but the success, however, depended upon the cooperation of the growers and on how far the order was implemented.

In 1949, four years after liberation, disposal of breeding places in Laguna province, particularly in San Pablo City and nearby municipalities, was done and to make this possible, the Bureau of Plant Industry alloted small sums of money from time to time and laborers were employed for the purpose. All dead coconut trees within the safe areas were cut down and burned or sawed for fuel and for other purposes. The piles of sawdust, rubbish, etc., were burned or scattered thinly on the ground. Up to December 1950, 4,057 dead trees were disposed off, and about 28,000 different stages of the pest were destroyed as mentioned above. As a result, the infested trees with riddled fronds in the neighborhood of the disposed dead trees, have greatly improved. The fronds are now almost normal and are about to bear fruit. In 14 places where control work was done in 1949–1950, of the 172 infested trees have still signs of the attack on the lower fronds in October 1953, showing a recovery of about 90 per cent after a lapse of about three years.

Trial with used gear oil as a repellant.—In 1948, four piles of decaying sawdust were placed side by side, in two rows two meters apart, each measuring 2 meters square and about ½ meter high. Two of the piles at opposite corners were sprinkled with used gear oil to form a coating over the surface. Application was done once a month for four months. They were inspected daily and after a week, holes were found almost everyday in the unoiled piles. A total of three adults of *O. rhinoceros* and five black crickets were found in the unoiled piles during the period while in the treated piles, no holes were observed. This seems to indicate that used gear oil, when regularly applied over piles of breeding media such as sawdust helps repel the beetles from laying eggs in them.

Trials with calcium arsenate, wettable DDT and air-slaked lime solutions against full grown grubs.—In September 1950, calcium arsenate, wettable DDT, and air-slaked lime solutions, each having a concentration of two level tablespoons (ordinary size) per liter of water were tried in two replications by pouring each solution separately into three decaying coconut stems standing, one meter high, with 6 full grown grubs in each. The same quantity of water was poured into the controls. The purpose of these trials is to determine whether any of these chemicals could be used to destroy grubs in decaying coconut stem as substitute for arsenate of soda, which was recommended by Mackie.

Results show that thirteen days after the treatment, calcium arsenate had a mortality of 83.3 per cent in the first set and 100 per cent in the second with an average of 91.66 per cent; wettable DDT had the same percentages of mortalities as calcium arsenate after 13 days in the two sets; air-slaked lime had mortalities of 50.00 and 66.66 per cent respectively, with an average of 58.33 per cent.

The two sets of control (water alone) had mortalities of 0 and 16.6 per cent respectively, with an average of 8.34 per cent. Calcium arsenate and wettable DDT solutions have a difference of 83.33 per cent mortality over control and lime solution, 49.99 per cent. The first two solutions therefore are effective against *Oryctes* grubs based from such trials. At the Government price of ₱0.75 per kilo of calcium arsenate and ₱2.20 of wettable DDT at the time of the trial, the costs of the treatment (chemical alone) using a liter of solution per coconut stump were ₱0.005 and ₱0.013 centavos, respectively. Calcium arsenate and wettable DDT are safer to handle than arsenate of soda and are readily obtainable by the growers. (See Table V).

Trial with traps.—Twenty three coconut trees killed by lightning stroke in the San Pablo Coconut Demonstration Station sometime in August 1950 were cut down after a month. In the cleared area, two rows of four holes each were dug, one meter square and one half of a meter deep. The holes were four meters away from each other in all directions. Two of the holes were filled (heapful) with sawdust, two with compost, two with rice chaff and two with small pieces of decaying coconut wood and bark. Before placing the said materials, they were examined carefully to be sure that they were free from any of the different stages of the pest. This observation lasted for three months, that was from September 1 to November 30, 1950. The traps found populated during the period were those two, which contained small pieces of decaying coconut wood and bark. One was visited once leaving 5 eggs, while the other was visited five times wherein 4 female beetles and 40 eggs were collected. Other traps had holes, but were not inhabited. It was suspected that the beetles also visited them, although oftener as in the case of sawdust, but went out again and transferred to traps with decaying coconut wood and bark which were preferred by beetles for egg laying at that time. (See Table VI).

Treating infested trees with sand.—This method is practical only in treating a few coconut trees planted in the backyards. Prior to World War II, black beetles infested trees in Manila and suburbs. I complained to the Bureau of Plant Industry and my two young coconut trees in my yard were treated by extracting the beetles with a flexible hooked wire and then enough fine sand, either pure or mixed with PDB crystals, was placed in between the petioles of the middle and upper fronds. In all cases the treated trees improved in stand as well as in fruiting and were never molested while the sand was there.

Natural enemies.—There are five species of *Hymenopterous* parasites reported by Thompson (1943) from other coconut growing countries, especially in the Dutch East Indies (Indonesia) but so far, Mackie and the writer had not the chance to observe any larval parasite from thousands of grubs collected and reared from different places. In June and July 1950, many adults of *Campsomeris aureicollis* were found abundant in a coconut plantation at San Pablo City feeding on flowers of sentimiento plants, *Stachytarpeta jamaicensis.* For curiosity, trial was done to see whether this species will work on the *Oryctes* grubs. Ten sets were used, each containing 10 grubs and 6 adults of *Campsomeris,* but none succeeded in all the cultures.

Mites have been observed on the grubs papae and adults but their presence seemed to have slight effect upon them especially upon the beetles. Larvae were attacked by an entomogenous fungus identified as *Metarrhizium amisopliae* Metsch., which was also reported by Mackie. Rats of the genus *Epemis* feed on the grubs. Crows and chickens feed on exposed young grubs as well as red ants. The writer suspected that Chinese sterling, *Atheopsar cristatellus,* and other birds that harbour or nest on top of tall dead trees, either feed on eggs and young grubs or scare the beetles, as in all cases no grubs nor beetles were found when said trees were cut. It is of interest to mention here that grubs and beetles are eaten by natives of Burma according to Ghosh (1923), and in the Philippines, some natives of Naujan, Mindoro, roast the grubs for food. Grubs are collected in the said province and sold at P4.00 a thousand to fishermen who use them as fish baits.

SUMMARY OF OBSERVATIONS

1. The black beetle, *O. rhinoceros* L., is one of the important pests of coconut in the Philippines and is seriously affecting those trees near sugar centrals, sawmills, in cities, towns and barrios where large piles of decaying sawdust, bagasse, garbage, animal manure and other decaying organic matters are found, in which the pest breeds in large numbers.

2. The beetle infests not only coconut but also other palms such as, buri, anahao, royal palm, etc., but the coconut is preferred.

3. Infested trees with about fifty per cent of their leaves damaged had about 1/5 as many nuts developing, as compared with normal trees, or a less in production of about 80 per cent.

4. The life cycle from egg to adult under laboratory conditions at San Pablo City, Laguna province, varied from 8.5 to 11 months with an average of 10 months or one generation a year. The broods, however, overlap.

5. Dead standing trees with about one half meter decaying at top end had an average of about 12 eggs, 7 grubs and 1 adult. As many as about 1,300 grubs were counted from a dead decaying tree of about 12 meters long.

6. Proper disposal of breeding media, trapping, treating stems with wettable DDT or calcium arsenate solutions, and applying sand either pure or mixed with PDB crystals at bases of fronds are effective measures against the pest. Used gear oil when coated over piles of sawdust at monthly intervals repels the beetles from breeding in them.

7. No larval parasite was observed so far, but the grubs are attacked by an entomogenous fungus, *Metarrhizium amisopliae* Metsch. Mites attack them especially the beetles, while field rats, crows, chickens and red ants attack the grubs.

REFERENCES

BANKS, C. S. The principal insects injuries to the coconut. Part 1., *Phil. Jour. of Science.* Vol. 1, (1906) 143-154.

BAPTIST, B. A. The control of insect pest of coconut. Papers read before the Coconut Conference, Colombo. (1947) pp. 38-44.

CORBETT, G. H. Insects of coconuts in Malaya. Department of Agri. Straits Settlements and Federated Malay States, No. 1, (1932) 36-48. (Kuala Lumpur).

FROGGATT, W. W. Pest and diseases of coconut palm. *Dept. of Agric., New South Wales, Science Bull. No. 2,* (1911) 47 pp. (Sydney).

GHOSH, C. C. The palm beetles in Burma with notes on other palm pests. *Bull. No. 19, Dept. of Agric. Burma* (1923) 1-30.

MACKIE, D. B. *Oryctes rhinoceros* in the Philippines. *Phil. Agric. Rev.* X, No. 4. Separate (1917) 20 pp.

SIMONDS, H. W. Pests and diseases of coconut palm in the Southern Pacific. *Dept. of Agric. Fiji, Bull. No. 16* (1925) 9 pp.

THOMPSON, W. R. A catalogue of the parasites and predators of insect pests. (1943) p. 84.

UICHANCO, L. B. Certain pests of coconuts in the Philippines, with suggestions for their control. Paper read before the First National Congress of Coconut Planters, Manila, February 24, 1930.

VIADO, B. C. and A. E. BIGORNIA. A biological study of the Asiatic palm weevil, *Rhychophorus ferrugineus* (Oliver), Curculionidae Coleoptera. *Phil. Agric.* Vol. 33, No. 1 (1949) pp. 1-27.

WESTER, P. J. The coconut, its culture and uses. *Phil. Agric. Rev.* Vol. XI. No. 1, (1918) 60 pp.

WOODWORTH, H. E. A host index of insects injuries to Philippine crops. (separate) *Phil. Agric.* Vol. X. (1922) pp. 9-35, 321-329 and Vol. XI. pp. 49-55.

TABLE I

LIFE CYCLE OF THE BLACK BEETLE, ORYCTES RHINOCEROS L., AS OBSERVED IN SAN PABLO CITY, LAGUNA PROVINCE

a. INCUBATION PERIOD:

YEAR	NO. OF EGGS	RANGE IN DAYS	AVE. IN DAYS	REMARKS
1947	17	12–17	14.63	Feb., Nov. & Dec.
1948	11	13–16	14.45	July
1950	7	14–18	16.17	June
1951	5	15–16	15.60	August

b. LARVAL AND PRE-PUPAL PERIOD:

YEAR	NO. OF GRUBS	RANGE IN DAYS	AVE. IN DAYS	REMARKS
1947	5	226–255	254.2	Sawdust
1948	3	271–290	280.5	"
1949	5	243–321	277.0	Coconut stem
1950	10	242–283	270.1	" "

c. PUPAL STAGE:

YEAR	NO. OF PUPAE	RANGE IN DAYS	AVE. IN DAYS	REMARKS
1947	13	18–22	20.61	Decaying sawdust
1949	5	20–24	21.60	" "
1950	7	21–28	23.70	" "
1951	6	15–20	17.50	" "

d. ADULT STAGE:

YEAR	NO. OF ADULTS	RANGE IN DAYS	AVE. IN DAYS	REMARKS
1947 1949	20	21–196	81.25	Failed to lay eggs.

TABLE II

POPULATION OF DIFFERENT STAGES OF THE BLACK BEETLE IN DIFFERENT BREEDING GROUNDS IN CERTAIN GIVEN AREAS

LOCALITY	BREEDING GROUNDS	NO. OF INDIVIDUALS	AREA COVERED	REMARKS
Calawan	Coconut trunk	126 grubs	2 m. long	old dead trees felled
San Pablo	”	121 grubs	1 m. long	2/22/47
		5 pupae		Lying down
		3 adults		1/22/47
” ”	”	31 grubs	2 m. long	Lying down
		333 grubs	3 m. long	Tree felled
” ”	Sawdust	27 eggs	⅔ m. high	12 m. long
		183 grubs	4 m. wide	within the coconut grove
” ”	”	82 grubs	⅔ m. high	” ” ” ”
		1 adult	1½ m. wide	
” ”	Carabao dung	18 eggs	½ m. high	Coral of carabao
		7 grubs		2/8/47
” ”	Rice chaff	none	1 m. x 4 m.	not decomposed yet decayed
” ”	Compost	96 grubs	2 m. sq. ½ m. deep	
” ”	Coconut stump	21 eggs	1 m. high	11/8/47
		6 grubs	½ decaying	
	”	9 eggs	”	”
		13 grubs		
		8 grubs		
	”	1 pupa	”	”
Alaminos	Pile of coir manufacture refuse	none	100 sq. m.	9/50
Los Baños	Dead buri trunk	18 grubs	2 m.	10/48
		2 pupae		

TABLE III

Population per Dead Tree as Observed in San Pablo Coconut Demonstration Station, San Pablo City, Laguna

Date Cut	Tree No.	Number of				Remarks
		Eggs	Grubs	Pupae	Adults	
9/1/47	1	6	7	0	1	
"	2	—	—	—	—	
9/3/47	3	42	28	—	2	
"	4	—	—	—	—	
"	5	32	38	—	1	
9/5/47	6	52	—	—	5	
"	7	—	36	—	3	
"	8	67	7	—	2	
"	9	25	—	—	2	Trees 15 to 20 meters high with about ½ meter of decayed wood from top end.
9/20/47	10	—	—	—	—	
"	11	—	35	—	3	
"	12	12	12	—	4	
9/23/47	13	11	18	—	4	
"	14	6	28	—	4	
9/29/47	15	—	21	—	—	
"	16	1	4	—	2	
10/3/47	17	37	4	—	—	
10/5/47	18	—	—	—	—	
"	19	6	3	—	1	
10/8/47	20	—	4	—	—	
"	21	—	—	—	—	
10/10/47	22	—	—	1	2	
10/11/47	23	—	6	—	1	
"	24	1	—	—	1	
"	25	2	—	—	1	
10/12/47	26	—	5	—	1	
"	27	9	—	—	4	
10/13/47	28	—	5	—	—	
"	29	40	14	—	1	
10/15/47	30	—	—	—	4	
"	31	—	3	—	1	
"	32	—	—	—	2	
11/19/47	33	—	—	—	—	
11/20/47	34	12	—	—	—	
"	35	15	7	—	1	
"	36	9	12	—	1	
11/24/47	37	6	—	—	—	
11/25/47	38	—	8	—	—	
"	39	—	—	—	—	
"	40	58	—	—	1	
"	41	13	8	—	—	
"	42	14	—	—	—	
12/2/47	43	28	—	—	1	
"	44	24	—	—	—	
"	45	14	—	—	—	
Total	45	542	312	1	56	
Average		12.26	6.93		1.24	

TABLE IIIa

NUMBER OF DIFFERENT STAGES OF THE BLACK BEETLE OF COCONUT, O. RHINOCEROS, COUNTED FROM DEAD TREES CUT IN SAN PABLO CITY, LAGUNA, DURING THE YEARS 1949 & 1950

BARRIO	NO. OF TREES	NO. OF DIFFERENT STAGES				RE-MARKS
		EGGS	GRUBS	PUPAE	ADULTS	
City proper	207	406	2,010	—	14	
San Ignacio	197	15	784	81	19	
San Nicolas	206	—	489	—	—	
San Rafael	496	1,185	1,288	63	166	
Concepcion	88	14	914	59	13	
Sto. Niño	208	—	2,248	34	81	
San Jose	172	45	1,139	4	8	
San Roque	862	2,597	6,547	149	401	
Sta. Elena	342	72	146	—	8	
San Lucas	112	223	436	3	29	
Sta. Isabel	40	—	127	—	17	
San Pedro	56	86	151	125	19	
Dolores	42	76	245	5	16	
Palakpakin	56	165	208	14	33	
Sta. Maria	21	53	33	—	3	
Del Remedio	100	180	63	18	41	
San Miguel	439	340	1,060	58	89	
Stmo. Rosario	110	2	922	787	40	
San Francisco	128	16	78	33	15	
San Gabriel	148	106	389	44	13	
San Gregorio	27	—	600	—	—	
Total	4,057	5,635	19,877	1,477	1,025	
Average		1.38	4.89	0.36	0.25	

TABLE IV

Number of Nuts that Developed and Developing from Different Clusters of 20 Non-Infested Trees, San Pablo City, Laguna

Tree No.	Bunch Number and Number of Nuts Developed and Developing															Height	Remarks
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	T	6-8 m.	
1	—	3	1	1	2	2	2	3	2	—					16		
2	2	4	5	4	2	5	3	4	3	—					32		All fronds normal
3	1	2	1	4	—	3	—	—	2	—					16		
4	1	4	1	2	4	2	4	5	—	3					26		
5	2	1	2	2	3	1	3	2	—	—					16		
6	—	3	3	2	—	1	1	2	—	—					12		
7	2	2	3	2	2	2	3	1	3	—					20		
8	—	2	2	3	4	2	3	3	8	—					27		
9	—	—	6	7	10	7	8	6	5	6	5	—			60		
10	3	4	3	3	4	4	4	1	—	3	—				29		
11	—	4	5	4	5	—	2	—	1	—	1				22		
12	1	2	1	1	4	3	4	4	3	2	3				28		
13	3	5	2	2	5	6	6	4	3	—	3				39		
14	5	3	4	1	1	3	4	2	—	—	1				24		
15	4	3	3	4	2	2	2	1	5	3	—				29		
16	8	4	6	8	4	4	6	5	2	8	2	—			57		
17	2	3	3	3	—	4	2	1	—	2					20		
18	—	—	3	5	1	2	2	—	1	5	2				21		
19	—	4	2	2	3	3	4	2	1	1	4	—			26		
20	—	1	1	2	5	3	1	3	5	1	2				22		
Total	34	54	57	62	61	59	64	49	44	34	23				542		

TABLE IVa

NUMBER OF NUTS DEVELOPED AND DEVELOPING FROM DIFFERENT CLUSTERS OF 20 INFESTED TREES, SAN PABLO CITY, LAGUNA.

TREE NO.	BUNCH NUMBER AND NUMBER OF NUTS DEVELOPED AND DEVELOPING															HEIGHT	REMARKS
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	T	6-8 m.	
1	2	3	4	2	0	0	0	0	—	—					11		
2	1	1	2	3	3	1	2	0	—	—					13		All fronds riddled
3	2	4	5	1	2	2	0	0	—	—					16		
4	—	—	3	0	0	1	0	0	—	—					4		
5	—	—	4	0	0	0	0	0	—	—					4		
6	1	—	—	2	0	0	0	0	—	—					3		
7	2	2	—	—	—	—	2	0	—	—					6		
8	1	0	2	—	—	2	5	0	0	—					10		
9	—	4	3	2	1	0	0	0	—	—					10		
10	—	—	3	0	0	0	0	0	—	—					3		
11	—	—	0	4	4	—	—	—	—	—					8		
12	2	—	1	1	1	—	—	—	—	—					5		
13	—	2	—	1	—	—	—	—	—	—					3		
14	—	3	—	3	2	—	—	—	—	—					8		
15	—	—	1	—	1	1	—	—	—	—					3		
16	—	—	—	—	—	—	—	—	—	—					—		
17	—	—	—	2	—	—	—	—	—	—					2		
18	—	—	—	4	—	—	—	2	—	—					6		
19	—	—	4	—	—	—	—	—	—	—					4		
20	—	—	—	1	—	—	—	—	—	—					1		
Total	11	19	32	26	14	7	9	2	—	—					120		

TABLE V

Effect of Wettable DDT, Air-slaked Lime and Calcium Arsenate Solutions upon Fullgrown Grubs of O. Rhinoceros, with Concentrations of Two Tablespoons (levelful) per Liter of Water

Date Treated	Treatment	No. of Grubs	No. of Grubs dead after		Total	% Dead	Remarks
			5 days	13 days			
Sept. 16, 1950 (1)	Cal. Arsenate	6	1	4	5	83.33	No further observations done because host already chopped during last examination
	Wet. DDT	6	4	1	5	83.33	
	Air-slaked lime	6	1	3	4	66.66	
	Water (control)	6	0	1	1	16.67	
Oct. 6, 1950 (2)	Cal. Arsenate	6	4	2	6	100.00	
	Wet. DDT	6	1	5	6	100.00	
	Air-slaked lime	6	0	3	3	50.00	
	Water (control)	6	0	0	0	00.00	

TABLE Va

Average Percent Mortality of each Treatment over Control, after 13 Days Observation

Treatment	% Mortality	% Difference Over Control	Remarks
Calcium Arsenate	91.66	83.32	
Wettable DDT	91.66	83.32	
Air-slaked lime	58.33	49.99	
Water (control)	8.34	—	

TABLE VI

Observations on the Attractability of Different Decaying Organic Matter upon Egg Laying, from September 1, 1950 to November 30, 1950

Date Found Inhabited or Suspected	Pile No.																Remarks
	1		2		3		4		5		6		7		8		
	No. of A	No. of E	No. of A	No. of E	No. of A	No. of E	No. of A	No. of E	No. of A	No. of E	No. of A	No. of E	No. of A	No. of E	No. of A	No. of E	
9/13/50	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—	
9/19/50	w/h	—	—	—	—	—	—	—	—	—	—	—	—	—	w/h	—	
9/21/50	—	—	—	—	—	—	w/h	—	—	—	1	26	w/h	—	w/h	—	
9/24/50	w/h	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
9/25/50	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	
10/1/50	—	—	—	—	—	—	—	—	—	—	—	—	w/h	—	w/h	—	
10/3/50	w/h	—	—	—	—	—	—	—	—	—	—	—	—	—	w/h	—	
10/8/50	—	—	—	—	—	—	—	—	—	—	1	7	—	—	—	—	
10/10/50	w/h	—	—	—	—	5	—	—	—	—	—	—	—	—	—	—	
10/16/50	—	—	—	—	—	—	—	—	—	—	1	4	—	—	—	—	
10/19/50	w/h	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
10/31/50	w/h	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
11/1/50	w/h	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
11/7/50	—	—	—	—	—	—	—	—	—	—	—	—	w/h	—	—	—	
11/12/50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	w/h	—	
11/14/50	—	—	—	—	—	—	—	—	—	—	—	—	w/h	—	—	—	
11/16/50	—	—	w/h	—	—	—	—	—	—	—	—	—	—	—	—	—	
11/18-30/50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Total	—	—	—	—	—	5	—	—	—	—	4	40	—	—	—	—	

Noted: A—Adult
E—Eggs
w/h—with holes only

ILLUSTRATIONS

PLATE I

FIG. 1.—Portion of a coconut grove at San Pablo City, Laguna province, showing the effect of shrapnels, machine-guns, etc., upon coconut trees during liberation (1945). Many trees died as a result.

PLATE II

FIG. 1.—Black beetle infestation near a big pile of sawdust, garbage, etc., in San Pablo City, Laguna province. Note the dead trees and those with riddled fronds as a result of the injury.

PLATE III

FIG. 1.—A coconut tree in the same plantation showing advanced injury by the pest.

PLATE IV

FIG. 1.—Male adult, dorsal view. Natural size.

FIGS. 1a and 1b.—Male adult, lateral view and annal end of abdomen. Natural size.

FIG. 2.—Female adult, dorsal view. Natural size.

FIGS. 2a and 2b.—Female adult, lateral view and annal end of abdomen. Natural size.

FIG. 3.—Egg, side view. Enlarged.

FIG. 4.—Newly formed grub. Enlarged.

FIG. 5.—Fullgrown grub, lateral view. Natural size.

FIG. 6.—Pupa, ventral view. Natural size.

PLATE I

PLATE II

PLATE III

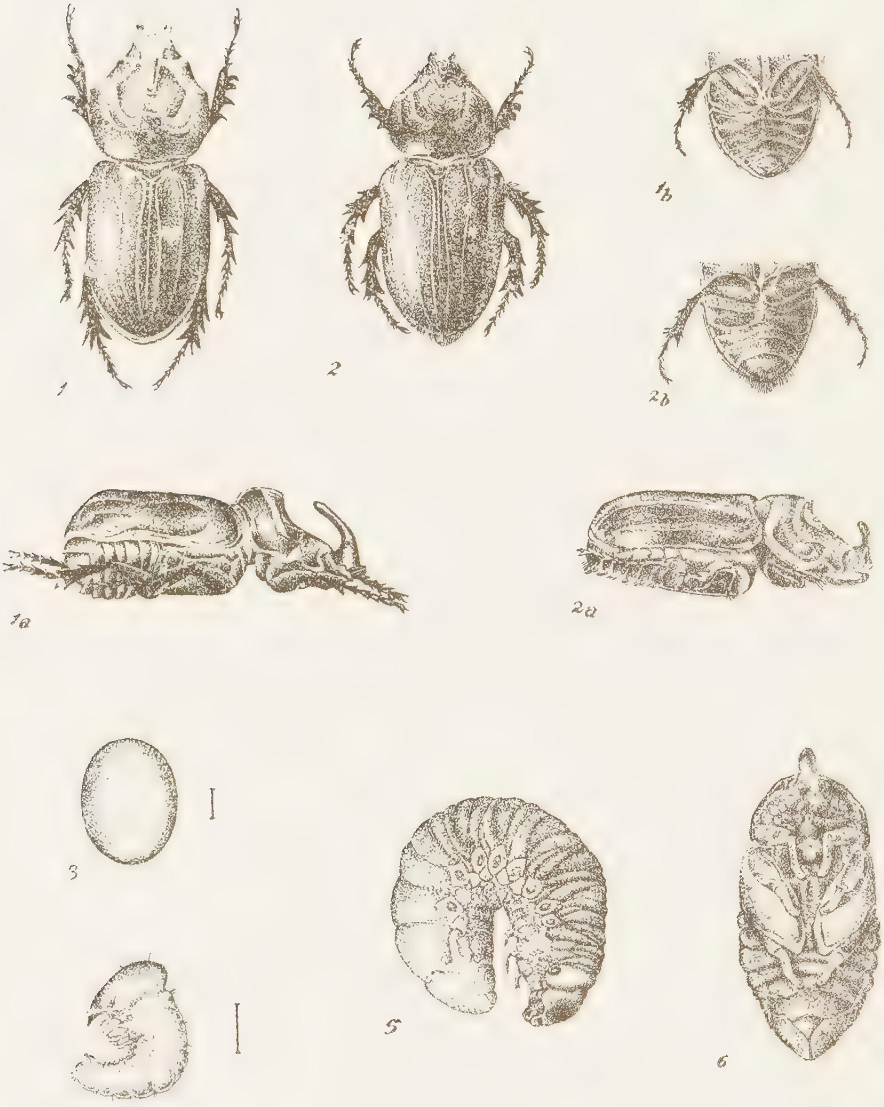

1
2
1b
2b
1a
2a
3
4
5
6

PLATE IV

RHINOCEROS BEETLES AS PESTS OF COCONUT PALMS

By J. Linsley Gressitt
Bishop Museum, Honolulu 17, Hawaii

The rhinoceros beetles constitute a large subfamily (Dynastinae) of the Scarabaedae. A considerable proportion of the rhinoceros beetles are associated with palms, while others feed in sugar cane or various fruits, flowers, fleshy plants, or vegetables, or suck juices from trees, during their adult stage. The grubs feed in various decaying vegetable materials or rarely in living plant tissue or on roots.

Throughout much of its range the coconut palm is attacked by one or more species of rhinoceros beetles. About 15 genera of the subfamily feed in palms (Lepesme, 1947). In the tropical Americas there are various species of the genus *Strategus* and others which are enemies of coconut palms. One of these kills seedling palms, whereas most species do their damage to more mature palms. The genus Oryctes, widely spread in the tropical and subtropical Old World, with some 42 species, is particularly associated with the coconut palm and other palms of economic importance. The principal home of the genus is in Madagascar and Africa, each of which possesses about 15 species, many of which are known to feed in coconut palms. Other species occur in the Mascarene Islands, Asia Minor, and southwest Asia, with one species in Europe. In tropical Asia and the Pacific area there are only four or five species, one of which, *Oryctes rhinoceros,* is by far the most important in the world. It feeds in a number of kinds of palms and other plants, but its favorite food is mature coconut palms, although the coconut palm is thought to be native to the New World.

The coconut rhinoceros beetle, *Oryctes rhinoceros* (Linnaeus), is thus an extremely important pest, being in many countries the most serious pest of the coconut palm, which is of such great economic importance. This beetle is native to most of tropical Asia, into the more strictly Asian insular areas, including much of Indonesia, the Philippines, Hainan Island, Taiwan and the southern Ryukyu Islands. In recent years it has been spreading in the Pacific area, and its importance has been growing. Over 40 years ago it reached Western Samoa, thence spreading to the rest of Samoa and to the Wallis Islands. Since the beginning of World War II it has found its way to the Palau Islands, New Britain, New Ireland, and recently Tonga and Fiji. Its damage in these islands has been extremely great and its presence in an important trading center like Fiji suggests the added danger of potential future spread to other Pacific islands.

This *Oryctes* has wide food tastes, for the adults are known to feed in the crowns of 32 genera of palms, as well as six genera of other families of plants, including *Agave, Pandanus,* sugar cane and pineapple. In the Palaus I found that a considerable population could be maintained in *Pandanus* when coconut palms were no longer present, and the beetles appeared to prefer *Pandanus* to very young palms. The grubs breed in the Pandanus plants killed by the adults, just as they do in the palm trunks. The grubs also feed in logs, stumps and roots of other dead palms and certain trees, and in sawdust, compost, garbage, manure, humus, straw and other dead plants or vegetable wastes. These facts are of considerable significance in relation to control because availability of abundant larval food where palms are present may greatly endanger the palms. Since this insect is very large, often measuring 50 mm. or more, it is difficult to control with insecticides. Baiting, trapping, repelling and other methods for the adult beetles have not been successful, and the only chemical treatment proven of value is the use of BHC (benzene hexachloride) against grubs in manure, compost pits or such accessible environments, and oiling or tarring of stumps, logs or lumber.

The adult beetle normally tunnels into the soft inner crown or "cabbage" of the palm, first forcing its way between petiole bases and then scraping and chewing its way into the tender portion, where it drinks the sap that flows. Though in the case of large population several adults may be found in the crown of a single palm, each generally makes its own tunnel. Feeding continues for some time, and after mating and a preincubation period of 10 or more days the female beetles deposit their eggs in available dead plant material. Adults may live four months or more and a female may lay over 100 eggs. The life cycle occupies about four months in favorable environments, and pupation takes place in crude cells of fibers, mud or in solid wood.

Within the normal Asian distribution of *Oryctes rhinoceros* there are apparently many factors which contribute to keep the beetle in check, including the presence of various natural enemies. These include predatory beetles such as ground beetles and certain elaterid and histerid beetles, centipedes, scorpions, crabs, toads, lizards, various birds, including fowl, ducks, woodpeckers, kingfishers and owls, and certain mammals, including some insectivores, rodents and swine. As to actual parasites, wasps of the genus *Scolia* attack species of *Oryctes* in Madagascar and Africa, but there is some question about the records of Asian

Scolia parasitizing *Oryctes rhinoceros.* This is a field which requires further attention, as does the question of natural enemies in general. *Scolia ruficornis,* a parasite of *Oryctes boas* in Zanzibar, was introduced to Western Samoa by H. W. Simmonds nearly a decade ago, though it has not proven very successful in Samoa. The same species was shipped by N. L. H. Krauss from Zanzibar to the Palau Islands in 1951, and in the spring of 1953 was found to be established in Palau by R. P. Owen and J. W. Beardsley. Taking into consideration the natural controlling agencies in Asia, outbreaks of *Oryctes* damage are generally correlated with factors upsetting the normal balance, such as felling of jungle, excessive accumulation of compost, manure or various sorts of plant débris. Another factor in Asia not present in the oceanic Pacific islands is the palm weevil. *Rhyncophorus ferrugineus* or its relatives, which follows *Oryctes* attack, laying its eggs in adult *Oryctes* feeding tunnels in the palm crowns, often killing palms where *Oryctes* alone might not.

When this *Oryctes* is transported to an oceanic Pacific island poor or lacking in many of the types of natural enemies and competitors and rich in larval and adult food, a very dangerous situation may result. This has now happened in various Pacific island groups, and perhaps the most notable example is the Palau Islands. The beetle is presumed to have reached Palau in 1942 from some point in southeast Asia. Following its introduction warfare resulted in the killing or damaging of many palms in the Palaus, thus providing an ideal situation for a "biological explosion". The large population which mushroomed with the excess of both larval and adult food, in the form of dead and living coconut palms, continued to grow as the beetles killed more palms. Not long after the end of the war the damage reached the point of destruction of nearly one-half of the coconut palms in the Palaus.

By 1951 the palms were exterminated from Angaur Island, except for new seedlings, which were being killed by the time they reached the age of three years, if not earlier. The beetle population, though reduced, is still maintained in *Pandanus,* so even the complete elimination of the seedling coconut palms would not exterminate the pest.

On Peleliu Island the coconut palms were exterminated on much of the island by 1951 and by the end of 1952 only a few living palms remained on an off-shore islet, and these were suffering from attack, and almost no nuts were being produced. In the southcentral Palaus coconut palms were exterminated on some islands by 1951 and on others were nearly gone, or suffering attack. In the central Palaus, where the beetle undoubtedly gained entry, the situation is like Angaur or on Peleliu, with the mature palms exterminated almost throughout, or some remaining in certain spots, but hardly producing any nuts.

In the northern Palaus, that is, north of southernmost Babelthuap, many fine groves of coconut palms remain in some areas, but in other areas damage has been very serious. In general, destruction of palms has been serious in all the villages, where warfare damaged palms and encouraged the beetle. Some of the coconut areas are isolated from others by jungle or mangrove, so the spread has been similar to jumping from one island to another, except where breeding in *Pandanus* or native palms has facilitated spread. In most of the village areas one-half or more of the palms were killed, whereas in isolated groves some are still not badly disturbed.

Probably all of the native palms in Palau are fed upon by the beetle occasionally, but the two most common species are slender and not as favourable food as most other palms. It would seem that the palm in the southern limestone islands was preferred to the common one in the Babelthuap jungles. On the other hand, fighting was much more intense in the southern Palaus, and this favored the beetle considerably. Kayangel Atoll, at the northern end of the Palau chain, did not receive the beetle until after the war, and the beetle is still spreading on the main island which it reached only a few years ago. As no abnormal excess larval food supply is present, it is not doing damage so serious as in the rest of the Palaus.

For two years a control crew under Mr. Owen has been circulating from one district to the next in Palau, clearing away dead palms and other surplus débris, and this is materially reducing the population of beetles, both by direct extermination and reduction of food supply. The circuit has not yet been completed, and a repetition will be necessary in some areas where a sizable population still exists or where breeding is taking place in compost or other materials. After this first major effort, the population will probably be reduced to the approximate status in Samoa, and further care and reduction of breeding materials, with the help of biological control, may reduce the problem to the point where copra production can again be profitable in Palau.

The loss of palms in Samoa, where the beetle has been present four times as long as in Palau, is at most one-quarter as great as in Palau, and the ecological factors in the two island groups are not greatly different, at least as far as natural enemies and competition is concerned. Even though *Scolia ruficornis* has not proved very successful in Samoa, the beetle would be only a minor problem there under average circumstances if the available breeding material could be kept at a lower level. Of course such grove sanitation is expensive, as it involves the removal of dead stumps and logs and the careful control of compost, manure and plant wastes. In Palau the stumps are cut off just above the ground, and the logs and stumps dragged to water by the use of water buffaloes. In other situations, including some of those in Samoa, the elimination of wood is not so simple, and burning may be necessary.

Much of the above information has been presented in greater detail in my report on this beetle (Gressitt, 1953). As regards the situation in the Pacific islands, much further work remains to be done on this pest, particularly as regards search for other natural enemies in southern Asia. Careful attention must be paid to quarantine in order to prevent further spread of *Oryctes* in the Pacific. The South Pacific Commission is employing two entomologists to work on the *Oryctes* problem.

As to other species of rhinoceros beetles attacking coconut palms in the Pacific area, there are a number in the Melanesian area. *Oryctes centaurus* Sternberg and *O. preussi* Kolbe have habits similar to those of *rhinoceros* but are not ordinarily abundant. Their natural enemies should be investigated. *Scapanes grossepunctatus* Sternberg does moderate damage to coconut in New Guinea, and *S. australis* has caused noticeable damage in New Britain. *Xylotrupes lorquini* Schaufuss (often called *X. gideon* Linn.) is frequently reported to damage coconut palms in New Guinea and New Britain, but its damage is of ordinarily minor importance, only harming the surface of new terminal shoots. Its close relatives elsewhere are probably of similar minor importance. *Trichogomphus semmilinki* Ritsema and *Papuana laevipennis* Arrow have also been considered important pests, and *Oryctoderus nanus* Arrow as a minor pest, of coconut palms in New Guinea (Froggatt and O'Connor, 1940–41). This *Oryctoderus* has been reported (Dun, personal communication, 1952) to feed on grubs of *Oryctes rhinoceros,* but it cannot be counted on for biological control as it also damages palms. Froggatt and O'Connor also reported the following species to damage young coconut palms in New Guinea: *Papuana semistriata* Arrow, *P. hübneri* (Fairmaire), *P. splendens* Prell, *Camelonotus (Dipelicus) ritsemai* Heller, *Oryctoderus latitarsis* Boisduval, *O. godeffroyi* Fairmaire. Other rhinoceros beetles were reported to damage *Caladium* and *Colocasia.* In the Solomon Islands *Trichogomphus semmilinki* Ritsema, *Scapanes grossepunctatus* Sternberg, and *Xylotrupes "gideon"* were said to be moderate pests of coconut and *Papuana laevipennis* Arrow a rare pest (Pagden and Lever, 1935).

In western Indonesia *Oryctes ngu* Mohnike (*trituberculatus* Lansb.) attacks coconut, but is much rarer than *rhinoceros. Xylotrupes* *gideon* Linn. or other species also cause some damage to palms and some other crops. In the Philippines and in Southeast Asia the latter species and some others also cause minor damage to coconut palms.

LITERATURE CITED

FROGGATT, J. L. and B. A. O'CONNOR. 1940. Insects associated with the coconut palm. I. *New Guinea Agric. Gaz.* 6(3): 16-32; 1941, II. *ibid.* 7(2): 125-133.

GRESSITT, J. L. 1953. The coconut rhinoceros beetle (*Oryctes rhinoceros*) with particular reference to the Palau Islands. *Bernice P. Bishop Mus. Bull.* 212: viii and 175 pp., 50 figs.

LEPESME, P. 1947. Les insectes des palmiers. Paul Lechevalier, Paris. 903 pp., 638 figs. (see pp. 446-487).

PAGDEN, H. T. and R. J. A. W. LEVER. 1935. Insects of the coconut palm and the present position of the coconut problem in the British Solomon Islands Protectorate. *Brit. Solomon Is. Agric. Gaz.* 3 (1): 2-22.

THE RHINOCEROS BEETLE AS A REGIONAL PROBLEM IN THE SOUTH PACIFIC

By L. J. Dumbleton
South Pacific Commission
Noumea, New Caledonia

In the original home of the Rhinoceros Beetle (*Oryctes rhinoceros*) and in other areas in which it has been present for a long period, the coconut management practices associated with a high density of human population and possibly also the presence of a more numerous and varied parasitic and predacious fauna tend, in normal times, to keep damage by this insect at a low level.

The present acute interest in the Rhinoceros Beetle in the Pacific arises principally from its accelerated rate of spread in recent years. Samoa became infested in 1910. In 1922 the beetle made a jump to Niuatoputapu in the Tonga group but was successfully eradicated. Wallis Island near Samoa became infested in 1930. During the recent war the beetle became established in New Britain and in the Palau Islands about 1942. In 1952 it was found in Vavau in the Tonga group and an attempt at eradication is proceeding. In 1953 it was found in Viti Levu (Fiji) and it has recently been identified from Netherlands New Guinea. In the Palau Islands and in New Britain the dead and damaged palms left in the wake of war favoured the rapid build up of large beetle populations and resulted in a heavy mortality of coconut palms. It must be emphasised however that the same result can follow, as it appears to have done in Wallis Island, if there is a relaxation of the sanitation measures associated with good coconut management practices.

In most parts of the South Pacific the coconut is not only of vital importance as a subsistence crop but is also the only or main cash crop.

Extensive new plantings of coconut are urgently required to correct the present preponderance of the older age classes and the actual or anticipated mortality caused by *Oryctes* in young plantings is an important factor delaying replanting in beetle infested areas.

No effective method of chemical control is known and if such were known the factors of cost and the availability when needed of the necessary materials and equipment might preclude its use. Biological control which would be an ideal solution under Pacific conditions has not so far given very promising results.

Until research has provided better weapons of control, reliance must therefore continue to be placed in plantation practices which reduce to a minimum the dead coconut logs and other material in which the beetle breeds and in the use of log traps, compost traps and hand collection of the beetle. The cost of the labour required for these operations is a considerable burden.

The problem in the South Pacific is thus:—

1. To prevent the further spread of the beetle;
2. To eradicate new infestations wherever possible;
3. To teach and put into practice the best existing methods of control;
4. To develop more effective methods of control.

The beetle is now present in some of the Pacific territories of all six member nations of the South Pacific Commission. Since it threatens both the subsistence and the cash economy of the people of the area the problem of its control is regarded as an urgent one and very suitable for action by the South Pacific Commission, as it is felt that co-ordination of research to obtain improved methods of control is needed.

Much work has already been done on the Rhinoceros Beetle both outside and inside the South Pacific area and with the increase in entomological staff in Pacific territories more can probably be anticipated. But the past efforts of individual Governments have been conducted independently to a large degree. The chances of success of future efforts will be increased considerably and appreciable economies of time and money will be effected if their individual efforts are co-ordinated or replaced by one unified scheme conducted by the South Pacific Commission.

Some work such as the biological control investigations must be done outside the area and other work requires continuity which the multifarious duties of the territorial entomologists leave them little time to undertake. The South Pacific Commission has therefore inaugurated an Oryctes Research programme which stresses those aspects which are more important to the South Pacific than to older infested areas where the beetle is already widespread or those which have not been adequately investigated. These fall into three main headings:—

1. Investigations into the biology and ecology of the beetle aimed at providing the basic information on its behavior which may point the way to improved practices in control, eradication and quarantine. A Commission entomologist has been appointed and is expected to commence work in Western Samoa in January, 1953.

2. Search in areas outside the South Pacific for possible controlling agents such as parasites, predators and diseases other than those which have already been tried. The Commission expects to appoint an entomologist shortly to conduct this work in South East Asia, India and possibly East Africa.
3. The testing of chemical attractants and the investigation of the attractant properties of materials extracted from the coconut palm. Some preliminary extractions of oils from palm crown and trunk have already been made.

No promise of a satisfactory solution can be given but the problem in the Pacific is serious enough to warrant an attack on it along what appear to be the most promising lines since existing knowledge of the behaviour of the beetle is inadequate for the formulation of more effective control measures. Any success which may be achieved will also be of great value to those countries outside the Pacific which suffer losses from the same insect. We cannot however depend on or afford to wait for the solution to the problem to be provided by work outside the area.

Lastly, it may be noted that the possible avenues for future work on this problem were discussed with members of the Invertebrate Control Consultants Committee of the Pacific Science Board at their Annual Meeting in Honolulu in February, 1953. The Commission's Rhinoceros Beetle programme is an amplification of the lines of work favoured by the above-mentioned Committee.

NOTES ON *ORYCTES RHINOCEROS* LINN. IN FIJI

By B. A. O'Connor
Department of Agriculture, Suva, Fiji

1. *History*. Since 1909, when the rhinoceros beetle was introduced into Samoa, it has constituted a threat to neighbouring island groups. Fiji sought to protect itself by quarantine measures, which were intensified when the pest was discovered in Vavau, Tonga, in February, 1952. However, the beetle had been established in Tonga for some considerable time before its discovery, in an area adjoining the wharf at Vavau. During this time there had been no quarantine on vessels proceeding from Tonga to Fiji.

When it became known that the beetle had been found in Tonga, considerable publicity was given to the pest in Fiji, with the object of familiarising the people with the beetle and its habits, and warning them of the possible consequences of its introduction. The finding of a living female beetle between the upper and lower tarpaulins covering the hatch of a vessel which berthed at Suva wharf outward bound from Apia caused considerable anxiety. This was on February 22, 1953, and on March 7 a living female beetle was found in a Fijian house at Suvavou, a village on the shore of Suva harbour.

Survey and eradication measures were immediately begun, time-honoured control methods such as destruction of potential breeding-places and setting up of compost traps being supplemented by a liberal use of B.H.C. The sum of £14,500 was made available by the Government for immediate use, checking points for inspection of vehicles were set up on the boundaries of the known infested area, and a system of inspection of vessels bound for other islands of the group was instituted. In June the checking points were dispensed with, as known infestation occurred beyond their location, and no beetles had been found on vehicles during the three months when the system was operating.

In the meantime, a tax of £2 per ton had been placed on copra, Government undertook to provide an equal sum, and merchants buying copra paid 1/8 per ton. It was calculated that about £12,000 per month would thus become available to fight the beetle. Expenditure is in control of a Board, with the Director of Agriculture as chairman and representatives of planters and merchants as members. A force varying between 100 and 200 personnel has been employed, which includes a senior inspector, inspector, a secretary, a storeman, foremen, drivers of motor vehicles, and a labour force. The labour strength includes survey gangs, gangs employed in making and examining compost traps, and teams engaged in destruction of potential breeding-places. The island of Viti Levu, on which Suva is situated, has been surveyed, and surveys of other islands of the group are being conducted.

As the known infested area extended, adjustments had to be made in the plan of campaign. The position at present is that Viti Levu and all the islands within five miles of its coastline have been declared an infested area. Within this area, owners and occupiers of land can be compelled to destroy potential breeding places. (It is fortunate that copra production on Viti Levu is insignificant). The main objects of the campaign now are to control breeding of the pest on Viti Levu and to prevent its spread to the copra-producing islands. The number of personnel employed is about 100. Inspection of properties and of shipping and aircraft is being carried on, large numbers of compost traps are being laid down, and survey work and destruction of breeding-places are continuing.

When the occurrence of the rhinoceros beetle in Tonga became known, the Fiji Government suggested to the South Pacific Commission that a research team should be appointed to study methods of control, finance to be provided by interested member countries. No immediate action was taken by the Commission. When the beetle was found in Fiji, another approach was made to the Commission, and Fiji guaranteed the whole of the cost of a research team for the first year. Mr. L. J. Dumbleton, Plant and Animal Quarantine Officer of the Commission, put forward a scheme of research involving the appointment of two entomologists and a chemist. The project was approved, and applications have been invited for the various appointments. It is hoped that work will begin in the near future.

2. *Incidence of Oryctes in Fiji.* The incidence of the beetle in Fiji is peculiar. One might have expected severe damage and high populations in the area where infestation originated, with lighter damage and lower populations as one moved further away. This was so in Vavau, Tonga, when the beetle was first found there. In Fiji, though there is an area where it appears that the beetle first became established, the general nature of the infestation is light and scattered, with insignificant damage. During the six months in which control measures have been carried on with a force averaging over one hundred men only 817 grubs, 75 pupae, 142 adults and two batches of eggs have been found. Of these, 402 grubs, 29 pupae, 79 adults and the two lots of eggs have been found in an area about three miles in diameter, centred

two miles north of Suva. This is considered to be the original site of infestation. The remaining grubs, pupae and adults have been found in a coastal strip extending five miles east and 23 miles west of the centre. Recent feeding marks have been noted 10 miles northeast, and older marks 60 miles west and 50 miles north, all near the coast, the last-mentioned being doubtfully the work of *Oryctes*. Feeding-marks have also been seen 20 miles inland from the infested coastal strip. Despite considerable survey work, there has been no extension of the known breeding area during the last two months.

3. *Investigation on control measures.* The known methods of control of the rhinoceros beetle are unsatisfactory, especially where it is desired to deal drastically with a new infestation. The writer has long considered that a synthetic lure for the adults would represent a big step forward in control measures. This aspect of the problem will be studied by the research team to be appointed by the South Pacific Commission, together with methods of biological control. In the meantime it has been thought desirable to make an effort to find a type of compost which would be more attractive to the beetle than its natural breeding places, and to treat this with a sufficient dosage of insecticide to kill the beetle. Nirula *et al.* (2) have shown that cowdung treated with 50% B.H.C. dispersible powder (containing 6.5% gamma isomer) at the rate of 2 ozs. per 10 cubic feet does not repel the beetle, and is lethal to grubs for a period of several months. However, in Fiji, where we are attempting drastic reduction in populations of *Oryctes,* and restriction of its spread, it seemed desirable to aim at killing beetles which enter treated compost pits, so that they cannot escape to lay eggs elsewhere.

A full account of the experimental methods employed and the results obtained may be found in the Fiji Agricultural Journal. (3) A Summary of the results is as follows:

Adult beetles confined for 40 hours in compost treated at the rate of one pound per 10 cubic feet with 50% B.H.C. dispersible powder were all dead or moribund three days after removal from the compost, and all quite dead five days after removal. Lindane 16% dispersible powder at the rate of 7 ozs. per 10 cubic feet had a similar effect, except that it appeared slightly slower in action, and killed only 19 out of 20 adults. All the beetles in the B.H.C. treated compost were immobilized at the end of their 40 hours' confinement, and it was noted that a beetle immobilized by B.H.C. or Lindane rarely recovers. Dieldrin 18% emulsifiable concentrate used at the rate of 7 fluid ozs. per 10 cubic feet killed only 9 out of 20 beetles. No beetles died in the untreated controls.

Compost with which was mixed meat meal or coconut meal at the rate of 50 lbs. per 10 cubic feet proved more attractive to the beetles than compost containing the following ingredients: no added ingredient, cowdung, 3⅓ gallons of molasses per 10 cubic feet, a split coconut log resting on top of the compost, and megass (unmixed with compost).

Sawdust was found very satisfactory as a base for compost mixtures, being a homogeneous and readily available material in which *Oryctes* is known to breed, and appearing to remove much of the objectionable smell of B.H.C. Attraction of the beetle to the following was tested: Sawdust only, compost only, sawdust plus coconut meal, sawdust plus meat meal, sawdust plus coconut meal plus B.H.C., sawdust plus coconut meal plus Lindane, sawdust plus meat meal plus B.H.C., sawdust plus meat meal plus Lindane. The coconut meal and meat meal were used at the rate of 25 lbs. per 10 cubic feet of sawdust, and the B.H.C. and Lindane at the dosages mentioned above. Sawdust only and compost only caught the fewest beetles, and beetles freely entered the sawdust treated with insecticide. Mixed with sawdust, the insecticides appeared to produce a quicker knockdown than when mixed with compost. Many beetles were immobilized after one night in treated sawdust, and these subsequently died. A heavy total mortality of beetles occurred. More beetles entered sawdust treated with B.H.C. than that treated with Lindane. While the method of conducting the experiment did not permit strictly accurate comparisons to be made between B.H.C. and Lindane, it was obvious that beetles would freely enter B.H.C.-treated sawdust.

As a result of these trials, it was decided to lay down large numbers of treated sawdust pits in the field. Pits are dug 2′ 6″ square and 1′ 6″ deep. These are filled with sawdust, to which is added a little topsoil, 12 lbs. of coconut meal and one pound of 50% B.H.C. dispersible powder in about 8 gallons of water. Coconut meal was chosen rather than meat meal, as it is cheaper and more readily available. The proportion of coconut meal was reduced to 12 lbs. per 10 cubic feet to lower the cost.

Most of the tests mentioned above were carried out in a large cage, 15′ x 9′ x 7′ 6″, consisting of ¼ inch wire mesh on a framework of ½ inch piping. This rested on a concrete base. Two young coconut palms with the fronds cut short were placed in drums in the cage to serve as food. This cage proved quite useful and convenient.

4. *Notes on the bionomics of Oryctes.* No attempt has as yet been made to study in detail the bionomics of the rhinoceros beetle. However, during the course of the trials to determine the attractiveness of various types of compost not treated with insecticide, some observations

of interest were made. Individual beetles were marked by cutting one or two notches in various portions of the elytra. By using ten different situations on the elytra where notches could be placed, it was possible to mark up to 55 male and 55 female beetles, using one or two notches on each beetle. The ten marking places were referred to by letters of the alphabet from A to J, and records were kept of individual beetles by using the appropriate letters to describe each beetle. When a beetle was liberated in the large cage at dusk, and was found in compost the following morning, it was assumed that it had spent the whole night in the compost, and had not visited one of the potted palms to feed. (The procedure was to collect beetles from compost every morning, and liberate them in the cage every evening). Some support was given to this assumption by the fact that an individual beetle would commonly be found in compost for a number of consecutive days, and then be missing for several days, presumably feeding in the palms.

Observations made were as follows:

(a) Beetles, both male and female, spent about 30% of their time in in the palm-crowns, and 70% in compost. In the field, the figure for time spent in the palms would be lower, perhaps about 25%, as beetles still in the pupal cell, or newly emerged from it, would have to be taken into consideration.

(b) Individual beetles, both male and female, spent considerable unbroken periods in both compost and palm-crown. These periods were for compost one to twenty-seven days, and for palm-crown one to fourteen days. Individual beetles moved from compost to palm-crown and vice-versa an average of four or five times during a period of 32 days.

(c) Indications were that prolonged and intense attack by beetles on the palm-crown is nesessary to kill a palm directly. An average of 11 beetles fed in each palm in the large cage for a period of 32 days without killing the growing-points of the palms. Of course, disease organisms could very likely kill palms damaged to this extent. The palms concerned were of a dwarf variety, about four years old.

(d) Male and female beetles occurred in the palm-crowns in approximately equal numbers.

Other observations made with beetles kept in tins containing compost and portions of sugarcane as food were as follows:

(e) Beetles can survive for extended periods under these conditions. One male, which is still living, was captured in the field over five months ago.

(f) Beetles appear to consume very little food, though the sugarcane may at times be tunneled extensively. This observation fits in with the amount of damage done to palms in the large cage, the damage being much less than had been expected. It has been noted above that beetles may spend extended periods in compost without food, and beetles have been kept in tins for three weeks without food, and appeared quite healthy.

An observation on the flight range of *Oryctes*:

(g) For this we are indebted to Mr. T. M. Skerman, Oceanographic Officer aboard H.M.N.Z.S. "Lachlan." When the "Lachlan" was anchored off Apia, Western Samoa, 750 yards from the nearest point of land, three rhinoceros beetles flew aboard one night between 8 p.m. and 9 p.m. A specimen sent to me by Mr. Skerman proved to be a male.

5. *Predators on Oryctes.* Owing to the small numbers and limited distribution of the rhinoceros beetle in Fiji, there appears little scope at present for the introduction of parasites. However, it appeared worth while to import predatory beetles which can subsist on a variety of hosts. During May and June, by courtesy of Mr. N. L. H. Krauss and other members of the entomological staff of the Board of Commissioners of Agriculture and Forestry, Hawaii, shipments of predatory beetles were received from Trinidad. These comprised 5,000 *Histerids,* a mixture of the species *Leionota colombiana, L. quadridentata* and possibly a third species, and 125 *Elaterids* of the species *Pyrophorus pellucens.* Mr. Krauss stated that the *Histerids* were found in rotting coconut logs and banana trees, and that they devour weevil larvae of various species, including the Banana Weevil Borer, *Cosmopolites sordidus.* In Fiji, under insectary conditions, they fed on various *Scarabaeoid* larvae, including young, first-instar *Oryctes* larvae, as well as on those of the Banana Weevil Borer. Of the *Histerids,* 4850 were liberated in the field, and of the *Elaterids*, 90. Of 40 *Leionota* kept in the insectary and fed on various species of grubs, four are still alive after 4½ months.

Two species of *Histerids* introduced to Fiji many years ago will also attack the larvae of *Oryctes* in confinement. These are *Plaesius javanus* and *Pachylister chinensis.* The former has been found in decaying sago palm logs, a known breeding medium for *Oryctes.* In Samoa, Dr. J. L. Gressitt and Mr. H. W. Simmonds (1,4) collected *P. chinensis* under split coconut logs used as traps for *Oryctes,* and found that the beetles would devour young, first-instar larvae of *Oryctes* in confinement.

LITERATURE CITED

(1) GRESSITT, J. L. The coconut rhinoceros beetle (*Oryctes rhinoceros*) with particular reference to the Palau Islands. *Bernice P. Bishop Museum Bull.* 212: viii and 157 pp., 50 figs.

(2) NIRULA *et al.* Investigations on the pests of the coconut palm. Parts 1 and 2. *Indian Coconut Journal.* Vol. IV, No. 1, pp. 5-12 and 34-35, 1950 and Vol. IV, No. 2, pp. 49-56, 1951.

(3) O'CONNOR, B. A. The rhinoceros beetle (*Oryctes rhinoceros* L.) in Fiji. In the press.

(4) Unpublished report by Mr. Simmonds.

SMALL-SAMPLE TECHNIQUES IN THE ANALYSIS OF FRUIT FLY POPULATION PHENOMENA[1]

By Irwin M. Newell
Agricultural Experiment Station
College of Agriculture, University of Hawaii
Honolulu, Hawaii

In studies of field populations of an insect, the foremost requirement is the development of methods of obtaining a measure of the abundance of the insect. In the case of well-established species, these methods can be developed over a period of time to meet the needs of the situation. Here the probable objectives are to measure seasonal or local differences in abundance, or to determine long period cycles in a population. In any event, the methods finally adopted must be consistent with the requirements peculiar to the problem, the anticipated length of the study, and the personnel and facilities available throughout the period.

In the case of a newly introduced species reaching epidemic levels, however, the approach is likely to be quite different, and quite certainly so when the species is one of economic importance. The lack of suitable techniques for population study, coupled with the urgency of acquiring as much information about the insect as possible, usually results in an early intense concentration of efforts on selected phases of the problem, much of which is poorly oriented, lacking in perspective, and unnecessary. Later, with the urgency diminishing, along with staffs and budgets, the investigator interested in long-range aspects of population study finds himself encumbered with techniques which must now be modified to fit within his more modest time and financial allotments. What is worse, he cannot be certain that the data obtained by his modified techniques are at all comparable with earlier data. This means that small differences in population levels which appear after changes in methods must be held circumspect, although in reality they may have considerable biological significance.

Much of this is only natural, of course, and stems from our generally immature understanding of insect population problems, and the lack of techniques of analysis. No investigator can be held responsible for failure to anticipate all circumstances, especially when working with species, the biology of which is largely or totally unknown. Each case is different from all others in some respects, so it is to be expected that a certain amount of probing in the dark must be done on every population problem.

---

[1] Published with the approval of the Director of the Hawaii Agricultural Experiment Station as misc. Paper No. 54.

Following the introduction of *Dacus dorsalis* into Hawaii in 1945 or 1946, a comprehensive program of research was outlined by several agencies (Carter, 1950, 1952). One phase of this program was the evaluation of the influence of natural enemies of fruit flies, including those which were already present in Hawaii, and those which were to be introduced from other parts of the world. This could be logically developed only as an integrated study of the major factors influencing fruit fly abundance. It was necessary, first of all, to determine what these factors were, and then to develop techniques for measuring them. The writer, to whom this task fell, did not begin field studies in Hawaii until late in 1949, at which time the fly population was evidently past its maximum. Moreover, some of the most important factors were not recognized, and some of the techniques were not developed, until much later. As a consequence, many interesting facts about the early history of the population were irrevocably lost, and must forever remain a matter of conjecture. This paper is written with a view to helping others avoid this same loss, either with the same species in other parts of the world unfortunate enough to be invaded by it, or with other species in which the basic problems are similar. While we have an over-supply of books which tell us in remarkably similar detail how to analyze data once it has been obtained, too few writers have said anything about feasible methods of gathering reliable data in population studies in the field. It will be apparent that certain facets of the problem of populations of *Dacus dorsalis* in Hawaii are rather unique to that species and that region, but some of the underlying principles will be found generally applicable to a variety of insect population problems.

Measurement of Abundance of Adult Flies

Dacus dorsalis is one of those species for which we fortunately have a powerful and highly specific attractant, methyl eugenol. The rediscovery and evaluation (Steiner 1952) of the attractant properties of this compound made it possible to develop a trapping program that is both practicable and reliable. Previously, the only lures available were the fermenting lures and oil of citronella. The frequent servicing required of fermenting lures, in addition to the fact that they are subject to a number of largely uncontrollable variables makes them undesirable as a means of obtaining an index of the population density of *D. dor-*

salis. Citronella varies greatly in its methyl eugenol content, so that unless rigorous precautions are taken to standardize it, there is reason to believe that different lots may produce markedly different results in fly catch. Methyl eugenol, the principal attractant in citronella, is obtainable in relatively pure form, and consequently is less liable to introduce discrepancies of this nature. The fact that it attracts males of *D. dorsalis* from distances of the order of hundreds of yards, practically eliminates the influence of slight differences in trap position which can be so important in the fermenting lure traps.

In 1950, the writer designed and constructed a trap with methyl eugenol dispensing surface made of two squares of blotting paper having a total evaporating surface of 16 square inches. These paper surfaces are kept saturated at all times by wicks and a reservoir of methyl eugenol. This lure dispenser is enclosed in a cage, covered on two sides with glass, and on the other two sides with screen in which there is a small central opening to permit entrance, but prevent exit of flies. The bottom of the cage opens into a lower chamber in which is placed a five-gallon can partly filled with a low-grade oil (flushing oil). Sufficient benzoic acid is added to the oil to prevent the growth of molds. The entire trap is covered with a square of galvanized sheet metal large enough to keep out even heavy rains.

At the maximum population density in 1948, it is probable that in some areas even this 5-gallon trap would have required servicing more than once a month, but only on a few occasions in 1950 were any traps filled to near capacity. In practice the traps are cleaned out and the lure dispensing surfaces are replaced once a month. The catches are measured volumetrically, using a screen-bottomed graduate.

Eleven of these traps have been maintained on the island of Oahu since June, 1950, and these have been the most reliable source of information on relative adult populations during that time. It is most unfortunate, of course, that this record does not go back to 1947 at least, for it is not possible to state with any degree of precision just how the present population compares with the population at that time.

While the traps described here have provided a good record of the change in fruit fly abundance that has taken place over the past three years, in retrospect, the writer feels that a much larger number of traps (say sixty) with a restricted lure output would have provided a somewhat more representative (although perhaps no more reproducible) index than the eleven traps. These would be much smaller than the 5-gallon traps, of course, having at most a capacity of one gallon, and with a much smaller lure dispensing area—perhaps only two square inches (that is, utilizing a single piece of blotting paper one inch square) or even less. With proper design, these could be made in such a way as to be serviced in a fraction of the amount of field time required with the larger traps. If one of these smaller traps were placed at each fruit collecting station, there would be little appreciable increase in the amount of field time required to process sixty traps, as compared with eleven traps at present.

Measurement of Larval Abundance

For some purposes, an index of relative adult abundance may be adequate, but from the standpoint of one interested in population dynamics, the larval population is just as important. On the island of Oahu, the problem of measuring larval abundance is greatly simplified by the fact that probably 90 per cent or more of the larvae of *Dacus dorsalis* develop in wild guava fruits. The cycles of fly abundance for the island as a whole follow the cycles of fruiting of this host so closely that other hosts, for purposes of population studies, can be overlooked as a significant source of larvae.

The problem, then, is reduced to one of sampling the guava population, and the first question that presents itself is, what method of sampling shall be followed? There are two general methods of approach: (1) to make very intensive collections and studies within a few selected areas, say five to ten, and (2) to make very small collections of fruit at a much larger number of points, say 50–100. Without going into all the pros and cons, it can be stated that only the second method will give results which can be relied upon in interpreting general population trends. Fortunately, too, it is the one which is the more economical of time and resources.

On Oahu, we are now taking samples of only four ground fruits per month from each of sixty different stations scattered over an area of four hundred square miles covering the Koolau section of the island. From the standpoint of sample size, this appears to give infestation values which analysis shows are probably within ten per cent of the true mean for the stations selected. How representative this is of the island as a whole cannot be stated, but care was used in distributing the stations to encompass most types of local variation encountered in guava producing areas, so that the sampling is probably fairly representative as well as reproducible.

In the laboratory the fruits are dissected and the larvae removed to a blended papaya medium (Newell, van den Bosch, Haramoto, 1951). The fruits are held for about a week and inspected at least once every other day in order to recover larvae that were missed in the initial dissection. This is very important as it completely eliminates error due to sampling differences stemming from a number of sources, including varying degrees of adeptness on the part of different workers, differences in recoverability of larvae at different infestation levels, etc. One man working alone can complete the fruit collections and trap collections in four days in the field, and with the aid of a second man, the dissection, recoveries, and trap catch measurements can be completed in the equivalent of about eight man-days per month. This is hardly a prohibitive time budget to obtain a reliable measure of larval infestation, percentage parasitism, and fly abundance over an area of 400 square miles.

Measurement of Fruit Abundance

Larval infestation by itself is no measure of larval abundance, but has meaning only when considered in terms of larval populations. In order to measure larval populations, the abundance of fruits must be determined. The methods used here will vary widely according to the host species involved. In the case of agricultural crops, planting, yield, or marketing data are usually available; but when the principal hosts are wild, other methods must be developed.

In the case of guava in Hawaii, the writer developed a method of estimating fruit abundance based on yellow-ripe tree fruits. The observations were made, wherever possible, from a point just outside the area, and the fruit abundance was estimated according to the following scale.

0. No ripe fruit evident, even on searching.
2. Ripe fruit present, but found only on searching.
4. Ripe fruit evident without searching, but very light.
6. Ripe fruit moderately heavy on most trees, or a very heavy crop on scattered trees.
8. Ripe fruit everywhere, on nearly all trees, and trees heavily laden.

Numbers 1, 3, 5, and 7 were used in those cases judged to be intermediate between two alternatives. The descriptive aspect of this scale is very important, for it makes it possible for different workers to apply it independently with a far greater accuracy than is possible where a purely numerical and arbitrary scale is used. Arbitrary numerical scales which have meaning only to their originator should be entirely avoided at all cost.

Tests have shown that this is a natural scale, for as the index of fruit abundance increases from 1 to 8, the relative abundance of fruits on the ground increases logarithmically. For any given index of tree fruit abundance, the actual number of fruits on the ground per unit area will vary somewhat from one guava site to another, depending on density of stand and other factors. But with adequate observations, fairly precise estimates of the comparative abundance of fruit at various times of the year, or from year to year can be made using rapid visual estimates of tree fruits. When adequate controls are established, fruit production over very large areas can be estimated in terms of weight, or numbers of fruit per unit area, if desired. For many purposes, however, this is not necessary.

The scales of estimated indices (IFA), and relative fruit abundance (RFA) for guavas on Oahu are compared in Table I. The values for RFA are given as number of fruit per 100 square feet of guava stand in the areas in which the comparisons were made. It should be emphasized that no worker can adopt these values directly, even for guava. However, they are presented to illustrate the method and show the possibilities in rapid measurement of relative fruit abundance. It is important to note that the IFA values cannot be used directly for comparing fruit abundance; moreover, average IFA values are completely meaningless and should never be used for any purpose. Mean relative fruit abundance can be determined only by first converting each IFA value to RFA, and then striking a mean. To illustrate this, we may assume two partial fruiting cycles, A and B, in which the IFA values during three consecutive months were (A) 2, 5, 8, and (B) 5, 5, 5. Both give a mean IFA value of 5, but the RFA values show that the mean relative fruit production during cycle A was 18.5, and during B only 4.9.

TABLE I

INDEX OF FRUIT ABUNDANCE (IFA) AND RELATIVE FRUIT ABUNDANCE (RFA), BASED ON VISUAL ESTIMATES OF YELLOW-RIPE GUAVAS AND NUMBER OF FRUITS ON THE GROUND. FOR THE PARTICULAR AREAS STUDIED, THE RFA VALUES MAY ALSO BE READ AS NUMBER OF FRUITS PER 100 SQUARE FEET. CORRECTED SLIGHTLY TO FIT TRUE LOGARITHMIC CURVE.

IFA	0	1	2	3	4	5	6	7	8
RFA	0.0	0.22	0.47	1.03	2.24	4.87	10.59	23.04	50.12

In the present study of *Dacus dorsalis* on Oahu, fruit abundance is estimated at each trap and fruit collecting station, so that a quite reliable picture of fruit production for the island as a whole is obtained. The time required for this is insignificant since an estimate can usually be made upon approaching or leaving the station.

One other method which might be suggested for measuring relative guava abundance over very large areas is to establish permanent, well-marked counting squares in which counts of ground fruits are made at suitable intervals. Because fruit abundance in guavas may vary greatly from one tree to another within a given stand, about three squares should be established in each station. These should therefore be small enough that the total area will not impose an excessive burden on the observer making the counts. In the case of guava on Oahu, three squares 10′ x 10′ in most stands would probably provide an adequate index. One advantage of this procedure is that it eliminates individual errors in estimating tree fruit abundance. A disadvantage is that it cannot be applied except at sites which have sufficient level ground to permit the use of the permanent counting squares. Moreover, it would require somewhat more time than visual estimates of tree fruit abundance.

One important point should be made regarding those species for which no satisfactory trapping methods are available, but in which it is possible to get reliable measures of both infestation and host abundance. Here measurements based on larval populations should be just as reliable as good adult trapping data, and even better than measurements of adult populations obtained by traps of low efficiency. To measure larval populations of fruit flies it is essential to have some method of measuring relative fruit abundance.

Mortality in Different Stages of Development

Studies of the mortality inflicted in different periods of the life history of *Dacus dorsalis* usually require a somewhat more specialized approach. Generally some intensive studies in a smaller number of stations are necessary, although even here it is likely that rapid small-sample methods may give results just as reliable, and much more applicable to the population as a whole.

The writer's studies in Hawaii show that at the present time the greatest mortality of *Dacus dorsalis* occurs in the egg stage. On the average, between 70 and 80 percent of the eggs laid in guavas during the year are killed by microorganisms introduced by the parasite, *Opius oophilus* Fullaway 1951. This parasite was first recognized at the end of 1949 (van den Bosch and Haramoto 1951), and within a few months became the most effective parasite of *D. dorsalis* on Oahu. During this period great changes in egg mortality undoubtedly took place, but since no measurements of this factor were made prior to that time, the record of this change is lost. No study of populations of fruit flies, or virtually of any other insect for that matter, is complete without a study of egg mortality. This is especially so in the case of *Dacus dorsalis* in Hawaii, where this factor alone accounts for about three times as many host individuals as all other factors combined.

Because of the time required for finding and dissecting the egg lesions, and counting the eggs, most studies to date have been carried out using samples of five to fifteen fruits from a few selected stations. However, it is now felt that two-fruit or even one-fruit samples from a much larger number of stations may be of greater value. At present, two-fruit samples from 14 stations on windward Oahu are being dissected to study the marked seasonal changes in egg mortality which occur. Yellow-ripe tree-fruits are picked and wrapped to prevent damage. In the laboratory these are dipped in a 0.5 percent copper acetate bath to prevent decay, and held for two days to allow the eggs to hatch. Each fruit is then dissected, and held in a separate jar until all larvae have been recovered. Data recorded for each egg lesion are: (1) eggs counted, (2) eggs obviously dead, and (3) whether or not hatching had occurred. The number of larvae found is recorded for each fruit, The total number of eggs in each fruit is taken either as (1) the number actually counted, or (2) the number of larvae plus the number of obviously dead eggs, which ever is the larger. This is necessary in the case of very heavy infestations for the egg lesions will sometimes be found eaten out and the dead eggs or chorions scattered beyond hope of recovery. The larvae are reared on blended papaya medium, as in the case of the general infestation studies, to determine the percentage of larvae parasitized.

The writer would like to emphasize the great importance of initiating studies of egg mortality as early as possible in the history of the invasion of a region by any fruit fly, or in fact by almost any insect.

Studies of larval and pupal mortality are complicated by the great number of factors involved. Toxins synthesized by microorganisms in decaying fruit, drowning, and predators all combine to produce what is observed as mortality. Moreover, these factors operate at widely differing levels from one region to another, so that even very precise studies in one or two localities may give a distorted picture of overall larval mortality. Here again, the author would urge the use of small samples at a large number of stations in preference to lengthy and laborious studies at a very few. Samples of only two yellow-ripe tree fruits, dropped and exposed on the ground in suitable cages to recover emerging flies and parasites would likely be adequate if repeated at a large enough number of points. Tree fruits dissected to determine egg mortality would serve as controls.

The cages used in the fruit fly studies in Hawaii are pyramidal in form, constructed of fine screen. They are designed so that all emerging flies and parasites are caught in a jar containing a small quantity of very viscous, colorless oil. The addition of benzoic acid to the oil prevents decomposition of the specimens and eliminates the need for frequent checking; in fact no checking is really necessary until the cages are brought in from the field.

Conclusion

The foregoing account outlines very briefly some of the methods used in the analysis of fruit fly population phenomena in Hawaii. These techniques will be presented in greater detail, along with an account of the findings, at a later date. However, it is believed desirable to point out at this time some of the general procedures which may be of value to others engaged in population studies in other parts of the Pacific where this fly may gain a foothold. The most important of these, in the author's opinion, is the use of small-sample techniques in field studies of insect populations. In taking small samples at a large number of stations, it is true that precision at each station is of low order, and little confidence can be placed in observed differences from point to point. But increasing the size of the samples to a degree that would insure statistical reliability at each point usually necessitates a reduction in number of stations to a level where the applicability of the findings to the population as a whole is impaired. At the same time, there are very few types of information which can be gained from intensive studies at a few points which cannot be found just as reliably by employing small-sample methods at a large number of points. Certainly it is difficult to analyze data on a productivity basis when these data cover only a few stations, regardless of the degree of precision of the data.

In the fruit fly population studies in Hawaii, the entire island of Oahu is, in effect, being used as one plot. To obtain measures of infestation and parasitism, a single sample of 240 fruits (maximum) is taken each month, and local variations are largely ignored (actually the area sampled is divided into four sections of about fifteen stations each, and even these show striking and consistent differences in infestation). The insular nature of the sampling area effectively eliminates biotic influence from outside. On larger land masses, this same result can be obtained by expanding the sampling area to such a size that the influence of contiguous areas is reduced.

Davis and Wadley (1949) in a very valuable analysis of grasshopper survey methods concluded, among other things, that more accurate surveys, at reduced cost, might be made possible by using several counties as a survey unit rather than only one. They suggested consideration of restricted random sampling methods, such as are recommended here, in grasshopper surveys. The form of this restricted randomness was different from that employed in the oriental fruit fly studies on Oahu, as one might surmise from a consideration of the two problems. For one thing, fixed sampling points were not mentioned specifically, and may not be practical in grasshopper survey methods because of changes in crops from year to year. But wherever possible, fixed stations should be employed, as this eliminates one important source of error that is inherent in purely random sampling. This imposes upon the investigator the additional responsibility of selecting stations which are representative of the area as a whole.

In conclusion, two other points will be reemphasized. The first of these is that the investigator should adopt only carefully standardized techniques in which error due to individual differences in observers is minimized as much as possible. Changes in personnel can seriously impair the value of investigations in which techniques are so individualized that other workers cannot adopt them. The second point is that the techniques utilized for analyzing population phenomena should be designed with an eye to the future. They must be adequate, and yield representative results. They should also be sufficiently economical of time and facilities that there will be a reasonable probability that they can be continued over a long period of time. Methods utilizing small samples collected at numerous points over a relatively large area offer the greatest assurance in these respects. This is not a recommendation for a minimum effort in population studies, but for maximum comparability of data from beginning to end.

References Cited

Carter, Walter. 1950. The oriental fruit fly: Progress on research. *Jour. Econ. Ent.* 43(5): 677-683.

Carter, Walter. 1952. Recent developments in oriental fruit fly research. *Jour. Econ. Ent.* 45(2): 274-279.

Davis, E. G. and F. M. Wadley. 1949. Grasshopper egg-pod distribution in the northern Great Plains, and its relation to egg-survey methods. *U. S. Dept. Agr. Circular* No. 816, pp. 1-16.

Newell, I. M., Robert van den Bosch, and F. H. Haramoto. 1951. An improved method of rearing field-collected fruit fly larvae. *Proc. Haw. Ent. Soc.* 14(2): 297-299.

Steiner, L. F. 1952. Methyl eugenol as an attractant for oriental fruit fly. *Jour. Econ. Ent.* 45(2): 241-248.

van den Bosch, Robert and F. H. Haramoto. 1951. *Opius oophilus* Fullaway, an egg-larval parasite of the oriental fruit fly discovered in Hawaii. *Proc. Haw. Ent. Soc.* 14(2): 251-255.

A BIOLOGICAL STUDY OF *BACTROCERA UMBROSA* (FABRICIUS) (TRYPETIDAE, DIPTERA)

By S. M. Cendaña and P. P. Namocale
College of Agriculture, University of the Philippines
College, Laguna, Philippines

INTRODUCTION

Bezzi (1919) enumerated 22 species of fruit flies in the Philippines. Several of these species are destructive to a more or less considerable degree to Philippine fruits.

The species *Bactrocera umbrosa* (Fabricius) causes considerable damage to the fruits of nangka or jackfruit (*Artocarpus heterophyllus* Lam.). Fruits attacked by the fruit fly rot in spots (Fig. 2a), rendering them unfit for human consumption.

According to Bezzi (1919), *Bactrocera umbrosa* (Fabricius), which was described in 1805, is of wide distribution, having been described in Java (as *Dacus fascipennis* Wiedemann in 1819 and as *Bactrocera fasciatipennis* Doleschall in 1856), in Singapore (as *Strumeta conformis* Walker in 1857), and in New Caledonia and Australia (as *Dacus frenchi* Froggatt in 1909). In the Philippines it is found from the north to the southernmost portions of the Archipelago.

Uichanco (1934) mentioned that the fruits of nangka, when raised on the outskirts of forests, are severely damaged by *Bactrocera umbrosa*, while in thickly settled districts, as in Manila and its suburbs, the pest is relatively unimportant, the inference being that the pest is normally bred in wild fruits. At present the only way to successfully mature fruits in badly infested localities, as in the College of Agriculture fields in Los Baños, is to bag the fruits. Cruz (1949) found old newspapers to be effective bagging material.

The present paper is based on a research conducted from July, 1951 to August, 1952, in the Department of Entomology, College of Agriculture, University of the Philippines. The objects were (1) to study the life history and habits of *Bactrocera umbrosa* (Fabricius) and (2) to determine possible methods of controlling it.

METHODS OF STUDY

The studies on the life history were made on caged materials. Since there was no way to determine the instars by direct observation of the larvae in ecdyses, this was done by collecting samples of maggots daily from the time the eggs were hatched until the maggots dropped to the ground to pupate. These sample larvae were studied anatomically as whole mounts as well as stained material after they had been cleared in potash.

The habits of the adult were studied in the field. The host plants were determined by rearing out adult flies from infested fruits from the field.

Experiments on control measures were limited to testing the efficacy of a fruit fly bait and the possible use of DDT and methoxychlor as spray or dust on the fruits to prevent damage by the fruit fly, or kill the pupating larvae or emerging adults if applied in the soil.

The fruit fly bait was made by dissolving 100 grams of brown sugar and 6.5 grams of white arsenic in one liter of boiling water. In the laboratory the bait was dispensed to the flies on wads of cotton which were first soaked in the bait and then hung in the cage where the adult flies were enclosed. In the fields, small tin cans with a wad of cotton and partially filled with the poisoned syrup were nailed on the branches of the experimental trees. Plain brown sugar solution was used in place of the poisoned bait in the control lots. The effectiveness was judged by the number of undamaged mature fruits on the trees where the bait was placed as compared to that of the control trees.

For their efficacy in preventing fly damage on fruits, methoxychlor and DDT were applied either as dust or spray on the fruits. In the same tree, some fruits were sprayed or dusted with DDT, some with methoxychlor, and some were left untreated to serve as control; some fruits were not treated again after the first application, some were retreated every week until the fruits became matured, while some every 2 weeks.

To test the possibility of killing the larvae that fell to the ground to pupate, DDT was applied either on the surface or was mixed with the soil in rearing jars, and fully-grown larvae were allowed to pupate in them.

RESULTS

Host Plants

Fruits of nangka or jackfruit, *Artocarpus heterophyllus* Linn., were most badly infested by *Bactrocera umbrosa*. All the other fruits that were found to serve as hosts of the pest belong also to the genus *Artocarpus*. During the fruiting season of rimas (*A. communis* Forst.) in 1951, the fruits were infested, but the degree of infestation was rather moderate. About 30 per cent of the fruits on the trees were destroyed. The damage on rimas fruits was similar to that on nangka fruits, although once infested, rimas fruits dropped to the ground and became totally destroyed and unfit for human consumption.

Other fruits like camansi (*A. camansi* Linn.), marang (*A. odoratissima* Blanco), antipolo (*A. blancoi* Merr.), and carandieng (*A. rigida* Bl.), a recently introduced species, were likewise found infested by the pest. The degree of infestation in these species, however, was not as serious as in nangka and rimas. The sparseness of the destruction on marang, antipolo and carandieng may be due to the scantiness of the pulp and the presence of many long spines that are closely set together so as to make it difficult for the female fly to oviposit in the rind of the fruit. This is especially true to marang, where oviposition seems to be possible only in spots on the fruit where the fruit spines are abnormally deformed and short, or where the spines have been accidentally cut short or parted.

Life History

The eggs are inserted in the rind of the fruit of the hosts, with the use of the pointed ovipositor, which the female, by persistent effort, slowly inserts into the fruit between the bases of the fruit spines. The maggots that hatched from the egg developed inside and fed on the tissues of the fruit. When fully grown, the larvae came out of the fruit, dropped to the ground and pupated in the soil, to emerge later as adult flies, which mated and laid eggs after a few days. Two larval instars were detected.

Table I shows the incubation, larval and pupal periods. According to the table, the eggs hatched 5 to 6 days (average 5.4 ± 0.2 days) after oviposition. The larvae became fully developed and dropped to the ground to pupate 9 days after hatching. Pupation occurred one day after the larva had dropped to the ground, and the pupal period was 12 days. The total developmental period for both sexes ranged from 27 to 28 days, with an average of 27.4 ± 0.2 days for 345 individuals of both sexes.

1. *The egg.* (Fig. 7c).—Pearl-white, banana-shaped, widest at middle, gradually tapering at both ends. Chorion translucent and smooth. Length 1.5 mm. width at middle of egg where it is widest, 0.030 mm.

   The eggs are laid in the rind at the furrows between the spines of the fruit.

2. *The larva.* James (1947) stated that generally dipterous larvae pass through 3 larval instars. It was not possible to determine the instars in the present study by direct observation of larvae in actual ecdyses because the maggots burrowed into the tissues of the fruit. However, a study of the structure of the preserved samples

of maggots, which were collected daily from batches of eggs that were known to have been laid and hatched on definite days revealed only 2 instars through which *Bactrocera umbrosa* larvae could have passed. The first instar is of 3-day duration, and the second instar of 6-day duration (4th to the 9th day after hatching).

The first-instar larva has these characteristic features: (a) mandibles that are sickle-shaped and with distinct teeth on the inside edge (Fig. 3a) and measuring 0.165 millimeters long, (b) the apertures of the posterior spiracles measure about 0.030 millimeters in length, (c) the posterior pair of apertures are about 0.060 millimeters apart, and (d) the apertures of each posterior spiracle are placed closely one behind the other (Table II). The second-instar larva has the following consistent characteristic features: (a) sickle-shaped mandibles, which, however, are devoid of teeth on the inside edge (Fig. 3b), and measure 0.30 millimeters long, (b) the apertures of the posterior spiracles measure about 0.120 millimeters in length, (c) the posterior-most pair of apertures are about 0.120 millimeters apart, and (d) the apertures of each posterior spiracle are distinctly far apart, one behind the other (Table II).

The first-instar larva is 14-segmented, slender, and measures from 3.525 millimeters in length on the first day increasing to about 5.37 millimeters on the third day. The greatest diameter when one day old is 0.480 millimeters, increasing to about 0.750 millimeters when 3 days old.

The pseudopodia, compared with the general body surface, are much raised. In general morphology, the larva is similar to that of *Calliphora erythrocephala* (Meigen) as described by Ludwig (1949).

The second-instar larva shown in Figure 4a is 7 days old. It is ivory white, about 11.44 millimeters in length, thickest from the ninth to the eleventh segments, where the diameter is about 2.144 millimeters, tapering anteriorly from the ninth segment to the first apparent segment, which comprises the head. It tapers slightly from the eleventh segment to the last segment, which is half cut-off dorsally, leaving a sloping surface on which is located the pair of posterior spiracles. The above features are similar to the larvae of fruit flies described by Ellingworth 1912 a-b). Larvae that are 8 or 9 days old do not differ appreciably from the 7-day-old larva.

The head of the fully grown larva, when viewed laterally, is subtriangular, with two antennal lobes each surmounted by a one-segmented antenna; labium gibbous from the side, medially cleft when viewed ventrally, and provided with numerous transverse more or less parallel chitinous ridges (Fig. 3b) suggestive of a rasping organ. Mandibles are black, with tips protruding beyond labium. Pseudopodia, which are located between the segments, are not as prominent as in first-instar, and are provided with numerous fine spines arranged in irregular rows. Anterior spiracles on each side of the posterior edge of the third body segment have two portions: (1) a distal, expanded fan-shaped part with a row of about 17 short, squarely-tipped co-extensive spines, and (2) a peduncle or stalk, which is much narrower and shorter than the width of the expanded distal portion.

Immediately after hatching and under field conditions, the larvae began to feed at first on the soft tissues of the rind. As the larvae developed, however, they went deeper into the fruit and fed on the soft tissues of the pulp and sometimes on the seeds also. A yellowish-brown liquid oozed out from the portion of the fruit that was attacked. The rind of the attacked portion became brown and, later on, black. When this black covering of the attacked portion was opened, a deposit of yellowish or sometimes brown matter was found in profuse quantities. By putting the ears close to the attacked fruit, the presence of maggots inside would be detected by the characteristic faint but fairly audible noise that the larvae inside made as they burrowed and fed in the fruit.

Nine days after the eggs hatched, the larvae, which had increased in length from 3.5 millimeters, on the day of hatching, to 11.5 millimeters and in greatest diameter from 0.48 millimeters to 2.5 millimeters, wiggled their way out of the fruit through a tiny hole which they made through the rind of the attacked portion. Sometimes a number of exit holes were made to enable them to go out in numbers. The larvae went out through an exit hole one at a time. A larva came out of the exit hole head first and forced itself out of the fruit by peristaltic movement of the body. After squeezing itself through the hole, the larva bent itself end to end, and then with a sudden jerk it flipped itself bodily away from the fruit and fell to the ground to pupate.

When newly hatched, the larvae were generally white, but when ready to pupate they became yellowish. The degree of maturity of the host fruit seems to have much to do with the color of the maggots. Larvae that grew in immature fruits were white; those in mature fruits, cream yellow.

The fully grown larvae came out of the fruit and dropped to the soil for pupation anytime during the day. After dropping to the ground, they burrowed into the soil to a depth ranging from 8 to 15 centimeters and pupated. Within 10 to 12 hours after dropping from the fruit, the larvae did not move anymore and had assumed the long-oval form typical of puparia of trypetid flies.

3. *The pupa.*—The puparium was oval (Fig. 4b). At first it was brownish yellow, but it turned darker brown with age. The real pupa inside the puparium was white. The developing wings were dark and showed through the puparium as dark spots on each side of the anterior two fifths of the pupa. Average-sized puparium—6.0 millimeters long, 2.5 millimeters wide.
4. *The adults.*—Adult female (Fig. 6a), general color darkwood, brown, face lateral stripes of thorax, and scutellum lemon yellow. Size from 7.0 to 8.0 millimeters in length, with a wing spread of 14.2 to 18.00 millimeters.

Adult male (Fig. 6b): Size from 5.4 to 7.5 millimeters in length with a wing spread of 13.8 to 17.5 millimeters. Abdomen with five visible segments above as in female. Genital claspers as shown in Figure 10.

The adult flies did not begin to mate until they were at least 3 days old. Oviposition took place 4 to 5 days after copulation. Twenty-day-old fruits or fruits as small as 3 inches in diameter, had been observed to be susceptible to being oviposited in and successfully infested by the fly. The more mature the fruit was, however, the more susceptible it was to *Bactrocera* attack.

The females were observed to lay eggs late in the day, usually between five to six o'clock in the afternoon. No oviposition has been observed to occur earlier than five o'clock. A female fly may lay from 98 to 112 eggs, all of which is deposited in one oviposition.

Flies were observed to feed by licking the moisture on the surface of the leaves. The females were also noticed to turn around and lick the oviposition puncture after laying eggs. The flies were found to roost underneath the leaves of host trees.

Seasonal abundance of adult flies

The results of weekly counts of adult *Bactrocera umbrosa* in the fields during the progress of the experiments are shown in Chart 1. Adult flies were most numerous in the fields in December, maintaining their abundance through January to February; then they declined in number until they could hardly be found during the months of May and June. Subsequently they gradually increased until they reached the peak again in December. It is probable that the degree of abundance of the adults may be related to the seasonal availability of host fruits, although this point has not been investigated.

Natural Enemies

Although the hymenopterous parasite (*Phaenocarpa bactrocerae* Gahan) had been reported as having been reared from *Bactrocera um-*

brosa in the Philippines (Dammermann, 1929), no parasite was encountered on the nangka fruit fly in the course of this study. Perhaps the thickness of the host fruit had something to do with the relative absence of successful parasites on *Bactrocera umbrosa*, for after the eggs of the fly had hatched, the maggots burrowed into the mass of the thick fruit, thus giving very little opportunity for the small parasites to reach them with their ovipositor.

Staphylinid beetles were found in rotting nangka fruits attacked by fruit flies, but these were on almost dried-up fruits from which, by then, the fruit fly maggots had long dropped to the ground to pupate.

At least three species of ants were observed to prey on the fruit fly. The common red tree ants were observed to prey on the fruit fly. The common red tree ant (*Oecophila smaragdina* Linn. var. *subritida* Emery) seized and carried to their nests maggots that had dropped to the soil before these could burrow into the soil. In one instance, a female fly, which was in the act of ovipositing, was pounced upon and killed by workers of the ant. *Pheidologeton* sp. and *Odontomachus* sp. are two species of ground ants that killed and carried off maggots on the ground before these had a chance to burrow into the soil to pupate.

Control

The poison bait was effective in killing the flies in confinement, but was not effective in preventing infestations of fruits in the field.

Application of DDT in the soil did not affect adversely the pupating maggots or the emerging adult flies. Provided that they were prevented from contacting the treated soil after they had emerged, they lived as long as the flies that pupated in the untreated lot.

The results of the tests on the application of insecticides on the fruits are presented in Table I.

All of the fruits in the control or untreated lots were damaged.

Eighty-six and seven-tenths per cent of the fruits dusted only once with 5 per cent methoxychlor were damaged, 40 per cent of those dusted every 2 weeks as well as those dusted weekly were infested.

When methoxychlor was applied as a 5 per cent spray, 86.7 per cent of the fruits treated were damaged if sprayed only once, 46.8 per cent when the fruits were sprayed every 2 weeks and 26.7 per cent were damaged when the fruits were sprayed weekly.

From these results, it can be seen that there is a slight, although not quite satisfactory protection of the fruits when sprayed or dusted with 5 per cent methoxychlor even if weekly re-treatment was made.

Even with 50 per cent DDT, one dusting of the fruits did not effect sufficient protection. Treating the fruits every 2 weeks, however, prevented the flies from infesting the fruits.

SUMMARY

1. The pest, which seriously affected fruits of *Artocarpus heterophyllus* Lam. and *A. communis* Forst., also infested but to a lesser degree, fruits of *A. blancoi* (Elmer) Merr., *A. camansi* Linn., *A. odoratissima* Blanco and *A. rigida* Bl.

2. The eggs were laid in the fruit where the larvae fed and developed; when fully grown, the larvae fell to the ground to pupate in the soil.

3. Incubation period was 5 to 6 days; the larva fell off the fruit and pupated in the soil 9 days after hatching. The pupal period was 12 days, and the developmental period for both sexes was 27.4 ± 0.2 days.

4. Two larval instars were detected. The first stadium was 3 days and the second stadium, 6 days.

5. The adults mated 3 days or later after emergence, and oviposition took place 4 days or later after mating. Oviposition was late in the afternoon, about 100 eggs having been deposited by a female in one oviposition.

6. The flies were most abundant in December, January and February, and least so in May and June.

7. DDT on the fruits when applied weekly and biweekly before the fruits were infested (about a month old), was found effective in preventing fruit infestations by the fly, while methoxychlor which was used either as dust or spray, and applied weekly or biweekly before the fruits were infested (about a month old), showed some possibilities. Further tests on these insecticides to determine the most effective dosage and intervals of application are recommended.

8. Application of DDT in the soil did not affect adversely the pupating maggots or the emerging flies. Treating the soil underneath the trees can not, therefore, be recommended as an effective method of control.

LITERATURE CITED

BEZZI, M. 1919. Philippine *Dacus*. *Philippine Journal of Science*, 15: 411-443.

BRUES, C. T. and A. L. MELANDER. 1932. Classification of insects. *Museum of Comparative Zoology at Harvard College, Bull.* 78: 1-672. Fig. 1-1121.

CRUZ, S. R. 1949. Newspaper as a protective wrapper for jackfruits (nangka) against fruit fly (*Bactrocera umbrosa* Fabr.). *Philippine Journal of Agriculture*, 14: (3): 213-219.

DAMMERMANN, K. M. 1929. Agricultural zoology of the Malay Archipelago. 473 p., 178 figs. Amsterdam: J. H. de Busay Ltd.

ELLINGWORTH, J. F. 1912a. A study of the biology of the apple maggot (*Rhagoletis pomonella*), together with an investigation of the methods of control. *Cornell University Agric. Exper. Sta. Bull.* No. 324: 124-186.

ELLINGWORTH, J. F. 1912b. Cherry fruit flies and how to control them. *Cornell University Agric. Exper. Sta. Bull.* No. 325: 191-204.

ESSIG, E. O. 1942. College entomology. vii + 900 p. New York: Macmillan and Company.

JAMES, J. T. 1947. The flies that cause myiasis in man. *U. S. Dept. Agric. Misc. Pub.* No. 631: 1-175.

LUDWIG, E. C. 1949. Embryology and morphology of the larval head of *Calliphora erythrocephala* (Meigen). *Microentomology,* 14 (part 3), 75-111. Fig. 43-65.

UICHANCO, L. B. 1934. A 25-year balance sheet for economic entomology. *Philippine Agriculturist,* 23: 419-429.

TABLE I

DEVELOPMENTAL PERIOD OF *Bactrocera umbrosa* (Fabricius)

BATCH NO.	DATE EGGS LAID	EGGS HATCHED		LARVAE DROPPED TO THE GROUND		PUPATED		EMERGED		TOTAL DEVELOPMENTAL PERIOD	NO. OF ADULTS REARED	
		DATE	INCUBATION PERIOD	DATE	LARVAL DEVELOPMENT	DATE	DROPPING TO PUPATION	DATE	PUPAL PERIOD		MALES	FEMALES
	1952	*1952*	*days*	*1952*	*days*	*1952*	*days*	*1952*	*days*	*days*		
1	14–I	20–I	6	29–I	9	30–I	1	11–II	12	28	22	31
2	7–II	13–II	6	22–II	9	23–II	1	6–III	12	28	38	46
3	2–VII	7–VII	5	16–VII	9	17–VII	1	29–VII	12	27	41	45
4	6–VII	11–VII	5	20–VII	9	21–VII	1	2–VIII	12	27	22	27
5	10–VII	15–VII	5	24–VII	9	25–VII	1	6–VIII	12	27	30	43
Average for batch			5.4		9		1		12	27.4	30.6	38.4
Average for individuals			5.4 ± 0.2		9		1		12	27.4 ± 0.2		

TABLE II

Anatomical Features of the Larva of Bactrocera From the First to the Ninth Day after Hatching

FEATURES OBSERVED		AGE OF MAGGOTS IN DAYS								
		1	2	3	4	5	6	7	8	9
Whole larvae	Length (millimeters)	3.525	4.2	5.73	7.13	10.20	11.25	11.44	11.52	11.52
	Diameter (millimeters)	0.480	0.510	0.750	1.32	1.64	1.68	2.14	2.40	2.52
Man-dibles	Length (millimeters)	0.165	0.165	0.165	0.30	0.30	0.30	0.30	0.30	0.30
	Number of teeth	3	3	3	0	0	0	0	0	0
Posterior spiracles	Length of apertures (millimeters)	0.030	0.030	0.030	0.120	0.120	0.120	0.120	0.120	0.120
	Distance between last pair of apertures	0.060	0.060	0.60	0.120	0.120	0.120	0.120	0.120	0.120
	Apertures on each spiracle	closely bunched	closely bunched	closely bunched	widely separated	widely separated	widely separated	widely separated	widely separated	widely separated

TABLE III

COPULATION AND EGG-LAYING RECORDS OF ADULT *Bactrocera umbrosa*

FEMALE NUMBER	DATE EMERGED	COPULATION		LAYING OF EGGS	DAYS AFTER COPULATION	NUMBER OF EGGS LAID
		DATE	DAYS AFTER EMERGENCE			
	1952	*1952*		*1952*		
1	28–VI	2–VII	4	6–VII	4	114
2	2–VII	7–VII	5	11–VII	4	98
3	3–VII	8–VII	5	13–VII	5	102
4	4–VII	9–VII	5	15–VII	6	103
5	8–VII	12–VII	4	17–VII	5	100
6	12–VII	16–VII	4	22–VII	6	101
7	16–VII	20–VII	4	25–VII	4	99
8	17–VII	22–VII	5	28–VII	6	107
9	21–VII	25–VII	4	31–VII	6	109
10	24–VII	28–VII	4	3–VIII	6	112
Average			4.4 ± 0.2		5.2 ± 0.3	104.5 ± 1.8

TABLE IV

LABORATORY TEST ON THE EFFECT OF POISON BAIT COMPARED TO THE EFFECT OF SUGAR SOLUTION ON ADULT *Bactrocera umbrosa*[3]

TREATMENTS	NUMBER OF INSECTS USED	NUMBER OF INSECTS THAT DIED AFTER				
		6 HRS.	12 HRS.	24 HRS.	36 HRS.	48 HRS.
With bait	50	—	—	5	24	50
Control	50	—	—	—	—	—

[3] The insects in the control cage lived and survived as long as 19 days.

TABLE V

Efficiency of (1) Methoxychlor Dust, (2) Methoxychlor Spray, and (3) DDT When Applied (a) Only Once, (b) Weekly or (c) Biweekly in Preventing Fruit Damage by *Bactrocera umbrosa*

INSECTICIDES			CONTROL		a. ONE APPLICATION		b. BIWEEKLY APPLICATION		c WEEKLY APPLICATION	
			Total Fruits Used	Attacked Fruits	Total Fruits Used	Attacked Fruits	Total Fruits Used	Attacked Fruits	Total Fruits Used	Attacked Fruits
Methoxychlor dust		1	3	3	3	3	3	2	3	2
		2	3	3	3	2	3	2	3	0
		3	3	3	3	3	3	1	3	0
		4	3	3	3	3	3	0	3	2
		5	3	3	3	2	3	1	3	2
	Total		15	15	15	13	15	6	15	6
	Per cent			100		86.7		40.0		40.0
Methoxychlor spray		1	3	3	3	3	3	1	3	1
		2	3	3	3	3	3	2	3	1
		3	3	3	3	3	3	2	3	0
		4	3	3	3	2	3	1	3	1
		5	3	3	3	2	3	1	3	1
	Total		15	15	15	13	15	7	15	4
	Per cent			100		86.7		46.7		26.7
DDT dust		1	3	3	3	1	3	0	3	0
		2	3	3	3	3	3	0	3	0
		3	3	3	3	3	3	0	3	0
		4	3	3	3	1	3	0	3	0
		5	3	3	3	2	3	0	3	0
	Total		15	15	15	10	15	0	15	0
	Per cent			100		66.7		0.0		0.0

TABLE VI

Effect of Treatment of Soil with Gesarol on *Bactrocera umbrosa*

TRIAL	KINDS OF TREATMENTS	NUMBER OF LARVAE ALLOWED TO PUPATE	NUMBER OF ADULTS THAT EMERGED	LENGTH OF PUPAI STAGE (DAYS)	LONGEVITY OF ADULTS IN DAYS
1	DDT mixed w/soil	25	25	12.0	1.0
	DDT dusted on soil	25	25	11.5	1.0
	Control	25	25	12.0	18.0
2	DDT mixed w/soil	15	15	12.5	1.0
	DDT dusted on soil	13	13	11.5	1.0
	Control	12	12	11.5	19.0
3	DDT mixed w/soil	20	20	12.0	1.0
	DDT dusted on soil	18	18	11.5	1.0
	Control	20	20	12.0	18.0
Total	DDT mixed w/soil	60	60	12.1	1.0
	DDT dusted on soil	56	56	11.5	1.0
	Control	57	57	11.9	18.2

TABLE VII

Effect of Application of Baits on Trees upon Fruit Infestations by *Bactrocera umbrosa*

REPLICATION NUMBER	FRUITS ON CONTROL TREES			FRUITS ON TREATED TREES		
	Total Number	Damaged	Per cent Damaged	Total Number	Damaged	Per cent Damaged
1	12	11	91.7	20	17	85.00
2	19	17	89.5	16	10	62.5
3	11	10	90.9	9	6	66.7
Total	42	38	90.5	45	33	73.3

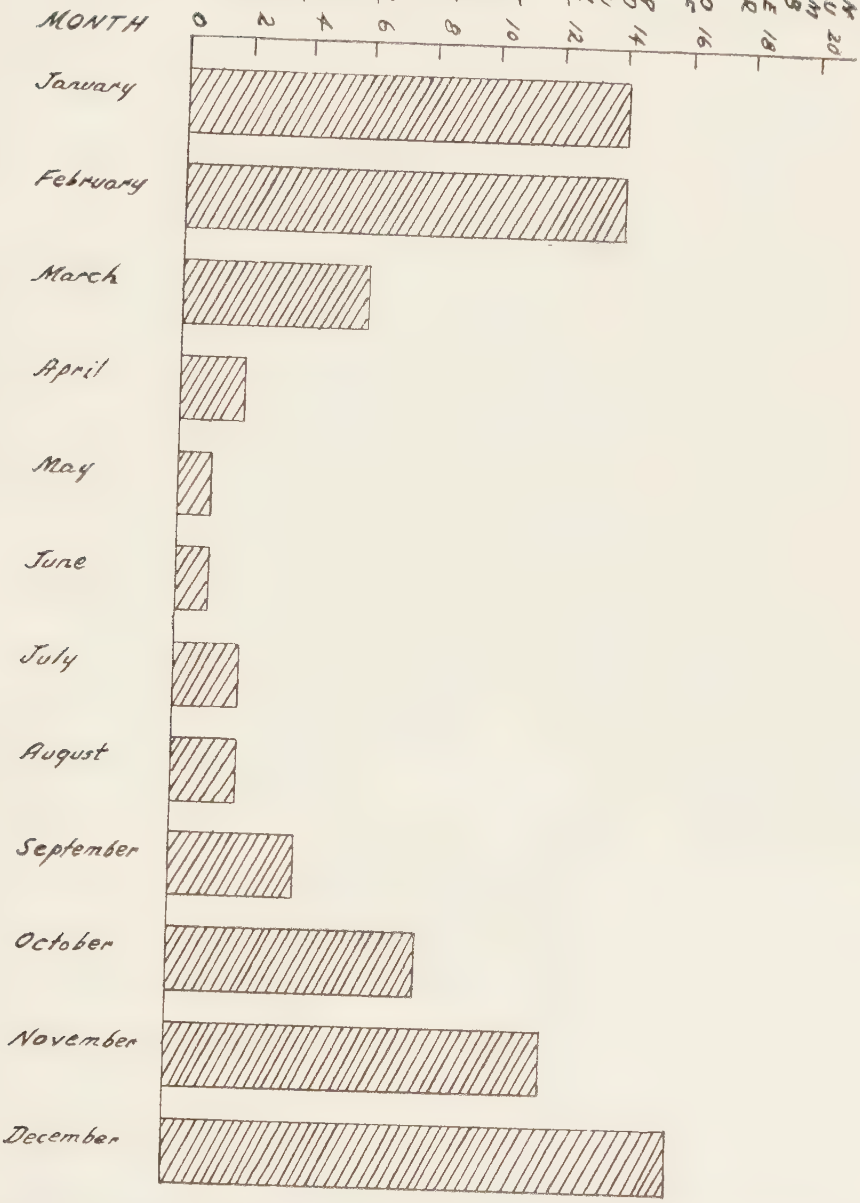


Chart 1.— Monthly abundance of adult flies (based on the weekly averages per fruit from twenty fruits) during the 1951-1952 fruiting season.

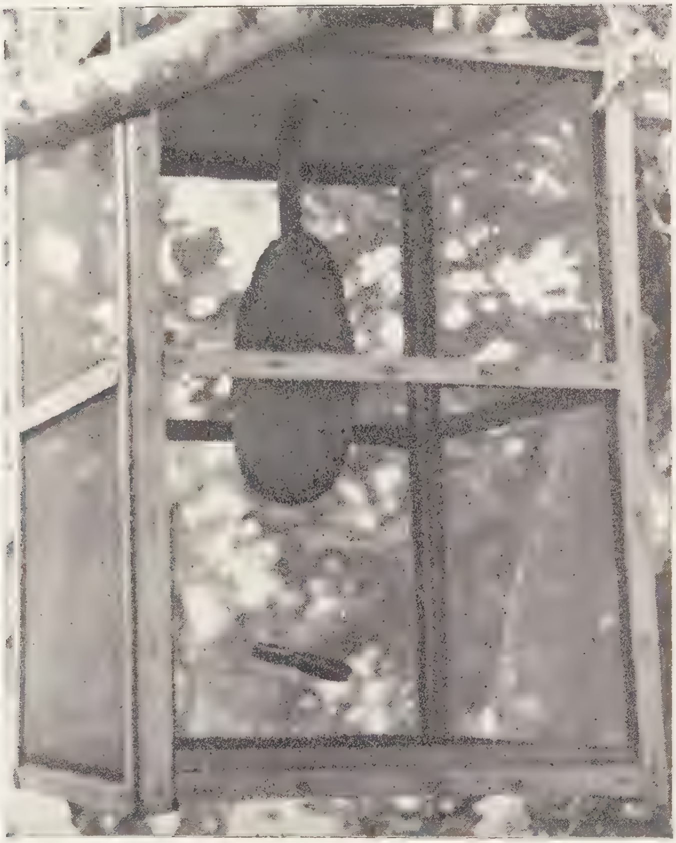


FIG. 1.—Breeding cage. (Photographed by Dr. J. Banzon, Photographic Division, College of Agriculture).

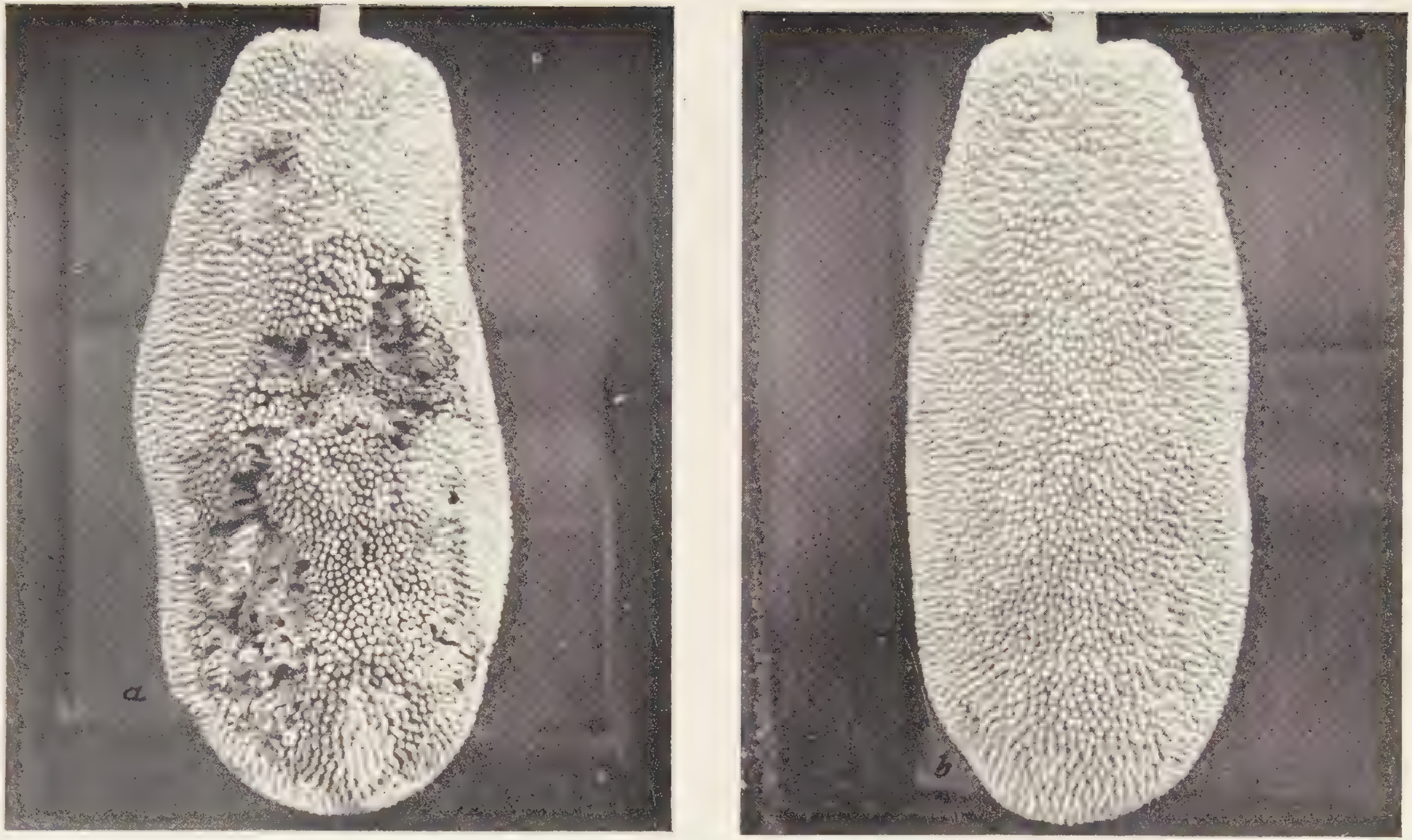


FIG. 2.—Nangka fruits: (a) Control, which was damaged by *Bactrocera umbrosa*, and (b) dusted with DDT, which remained sound. (Photographed by Dr. J. Banzon, Photographic Division, College of Agriculture).

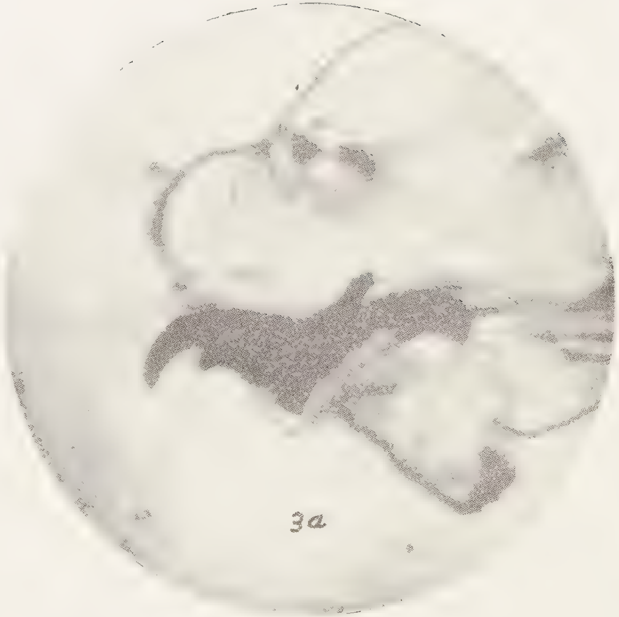


Fig. 3a.—Mandible of first-instar larva (x183). (Photomicrographed by Dr. J. Banzon, Photographic Division, College of Agriculture).

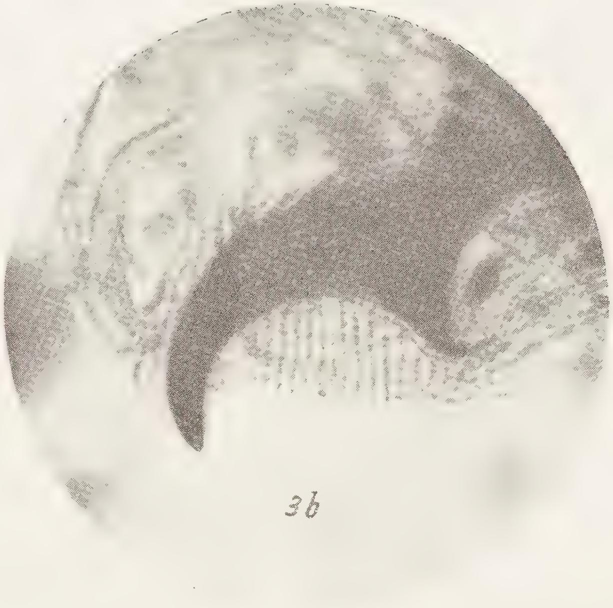


Fig. 3b.—Mandible of second-instar larva (x183). (Photomicrographed by Dr. J. Banzon, Photographic Division, College of Agriculture).

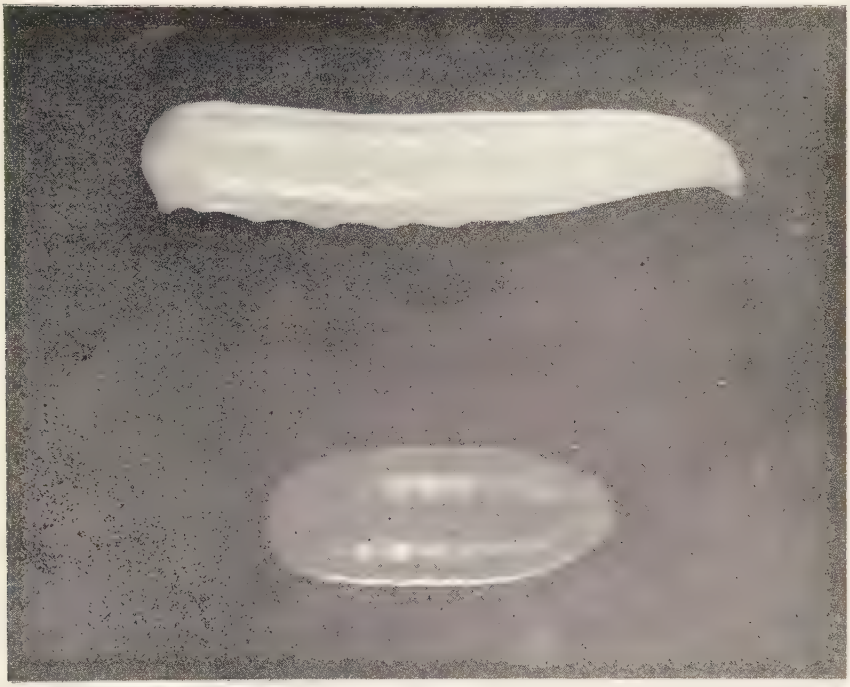


FIG. 4.—(a) Second-instar larva (x8); (b) puparium (x8). (Photographed by Dr. J. Banzon, Photographic Division, College of Agriculture).

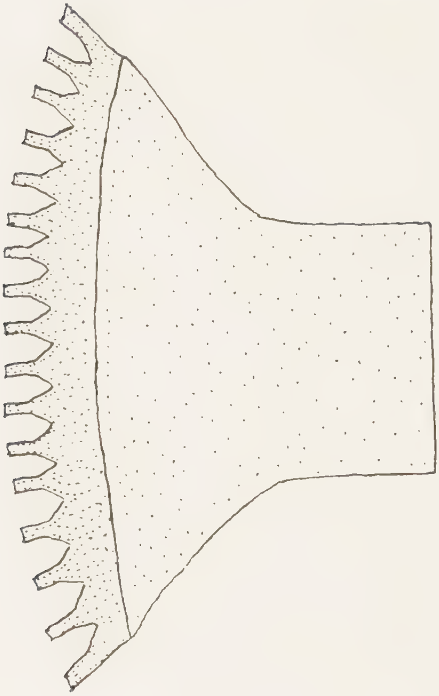


FIG. 5.—Free-hand drawing of anterior spiracle (x600).

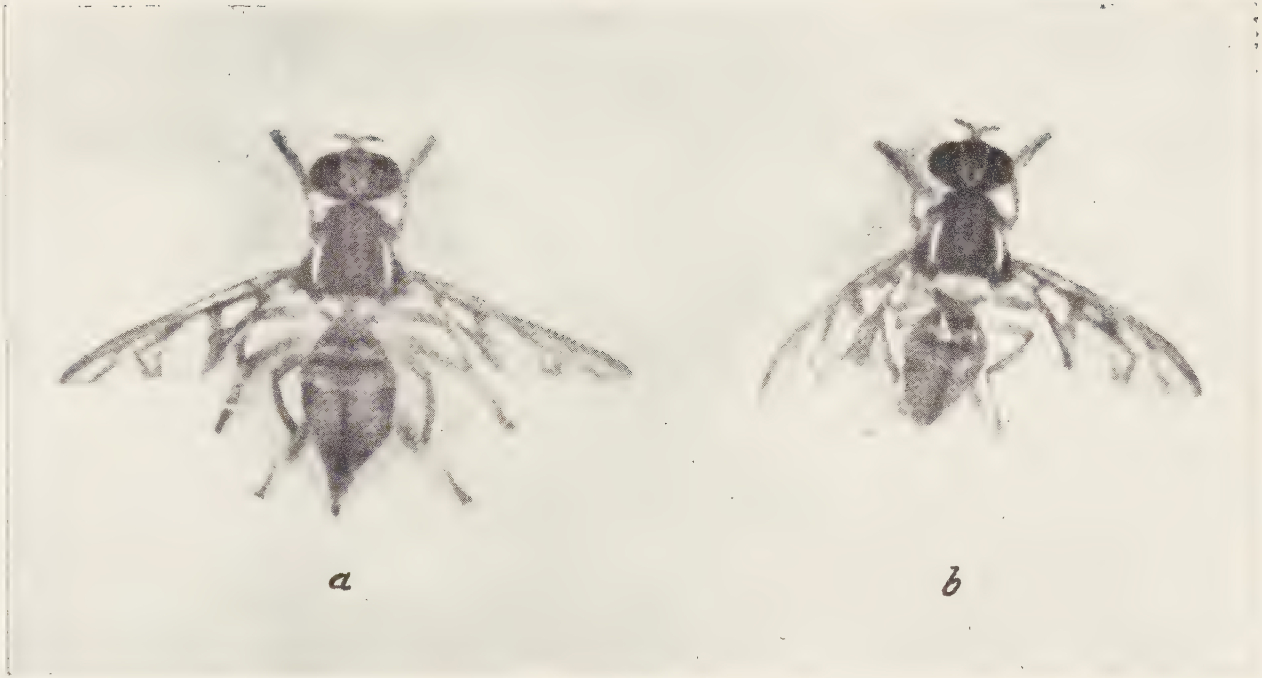


FIG. 6.—Adults: (a) female, (b) male (x5). (Photographed by Dr. J. Banzon, Photographic Division, College of Agriculture).

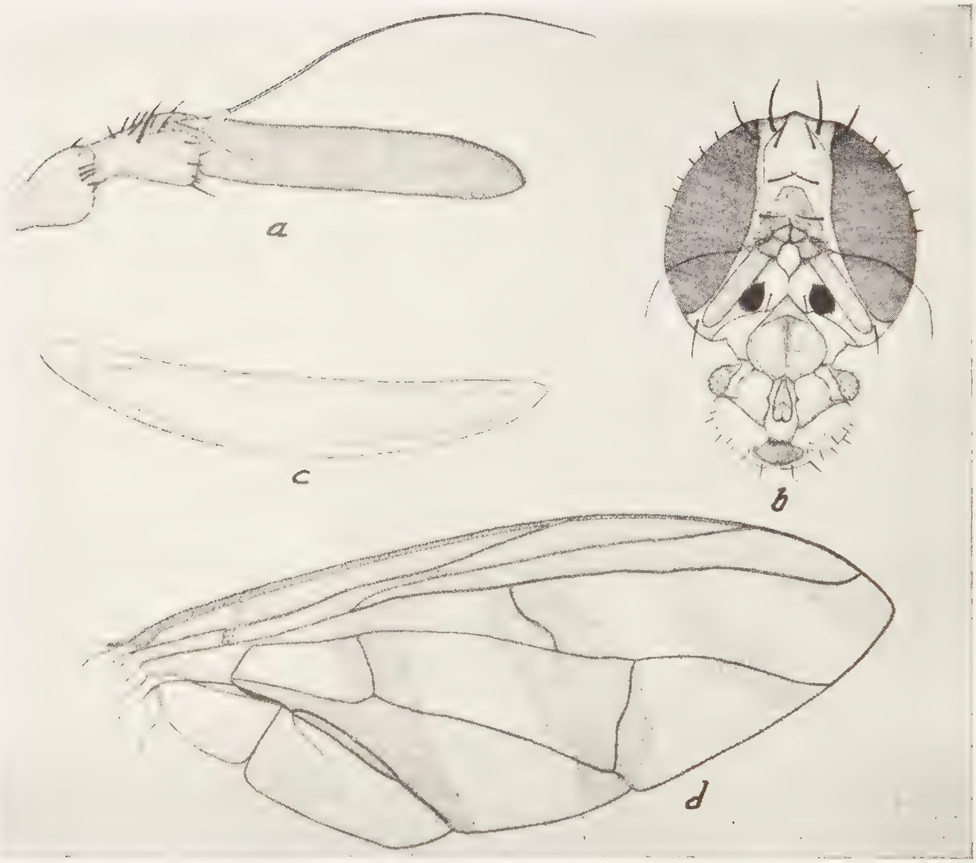


FIG. 7.—Camera lucida drawings of: (a) antenna (x53); (b) head of female, anterior aspect (x23); (c) egg (x50); (d) wing (x15). (Photographed by Dr. J. Banzon, Photographic Division, College of Agriculture).

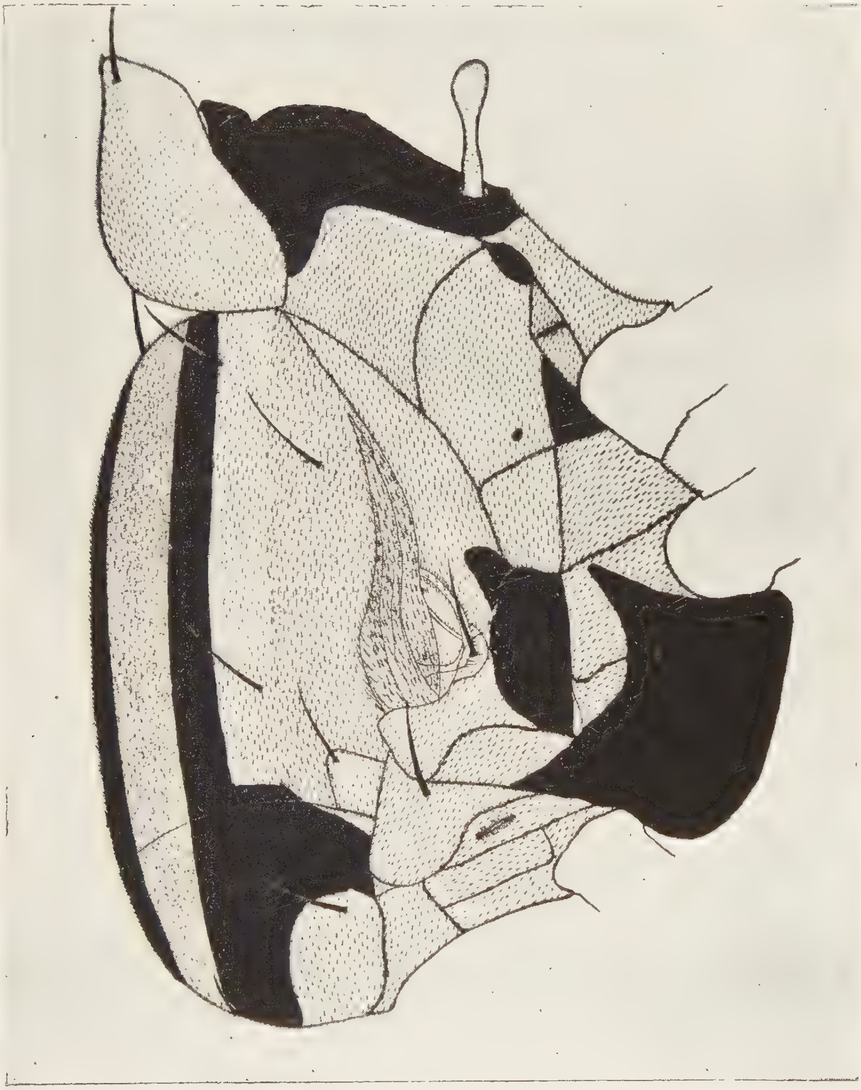


FIG. 8.—Freehand drawing of: thorax of female, lateral aspect (x50). (Photographed by Dr. J. Banzon, Photographic Division, College of Agriculture).

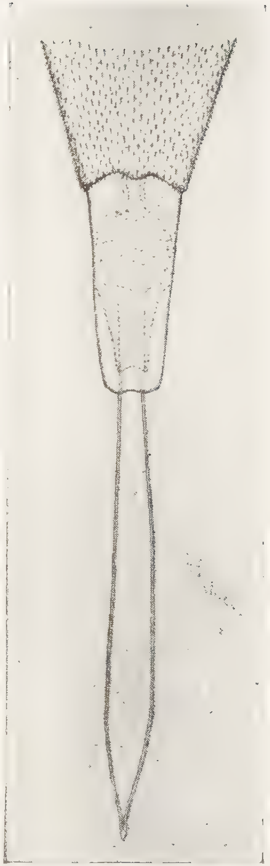


FIG. 9.—Camera lucida drawing of ovipositor, dorsal aspect (x382). (Photographed by Dr. J. Banzon, Photographic Division, College of Agriculture).

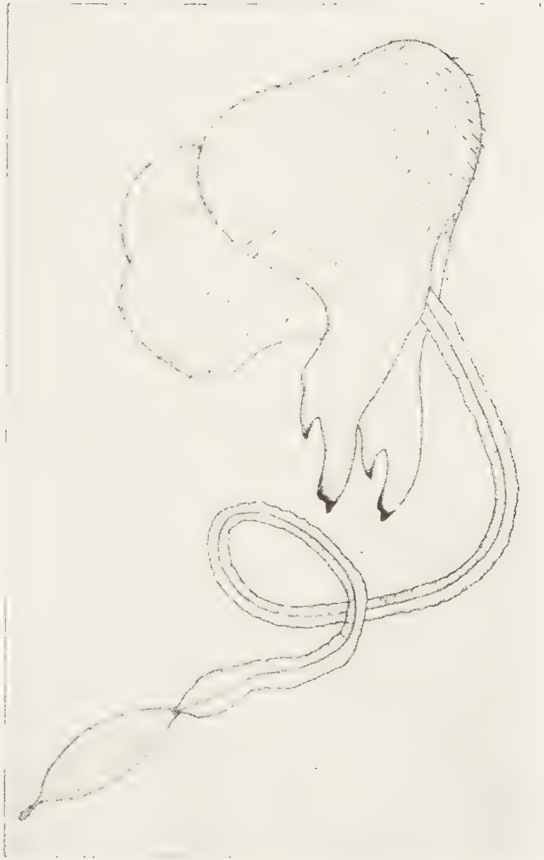


FIG. 10.—Camera lucida drawing of genital claspers (328). (Photographed by Dr. J. Banzon, Photographic division, College of Agriculture).

OBSERVATIONS ON THE RHINOCEROS BEETLE *ORYCTES RHINOCEROS* IN MALAYA

By T. R. Gardner
Bureau of Entomology and Plant Quarantine
Agricultural Research Service
United States Department of Agriculture
Beltsville, Maryland, U. S. A.

Several years ago I was sent to Malaya by the Pacific Science Board of the National Research Council to search for natural enemies of the rhinoceros beetle, *Oryctes rhinoceros* L., for introduction into the Palaus, a group of islands in the Western Carolines. This beetle, which became established in the Palaus during World War II, had become a very serious pest of the coconut palm, *Cocos nucifera*, a plant important to the economy of the natives in that area of the Pacific. En route to Malaya from Guam I made short stops in the Philippines and Siam to search for natural enemies of the beetle, but none were found.

Headquarters was established the latter part of December 1947 at Kuala Lumpur, capital of the Federation of Malaya, and laboratory facilities were provided by the Department of Agriculture. Because of the rainy season little field work was accomplished until about the middle of January 1948. For the next six weeks an intensive search was made for the natural enemies of the rhinoceros beetle in the coconut producing areas within a radius of about 50 miles from Kuala Lumpur. While searching for natural enemies of this beetle observations were made on its abundance, injury to palms and control measures as practiced in Malaya.

Although the adult rhinoceros beetle, sometimes called the black beetle in Malaya, prefers the coconut palm, it also was observed on the oil palm, *Elaeis guineensis*, the areca palm, *Areca catechu*, and the nipa palm, *Nipa fructicans*. Other palms reported damaged by the adult in Malaya are the nibong palm, *Oncosperma tigillaria*, and the sago palm, *Metroxylon sagu*.

Some injury to the coconut palm was observed in plantations and estates Southwest of Kuala Lumpur towards Port Sweetenham and Carey Island and North from Klang towards Kuala Selangor. The most noticeable injury was in small scattered plantings around and near villages. In no case, however, was the injury to palms anywhere near as bad as that observed in the Palau Islands and on the Island of Luzon in the Philippines. It is quite probable that the injury to palms in some areas was due to the build-up of the beetle during the War when little or no control measures were practiced. Injury to the coconut palm by the weevil, *Rhynchophorus schach* Oliv. was noticed occasionally. This is characterized by the falling of the central shoots of the palm. This weevil lays its eggs in the holes and tunnels in the crown of the palm made by the adult rhinoceros beetle. The feeding larvae of this weevil often cause the death of the palm.

The general absence of serious injury to the coconut palm by *O. rhinoceros* in Malaya is due, undoubtedly, to the education of the people of the seriousness of this pest, to the enforcement of control measures and to its natural enemies. One method of educating the people is through the distribution of posters. These illustrate a damaged coconut palm leaf or frond, a damaged palm tree, and a leaf stalk with holes and tunnels caused by the adult. It also shows the egg, larval, pupal, and adult stages of the beetle. The media in which the beetle breeds are listed and simple control measures are given. The posters are printed in four languages. Control measures require the destruction of all dead palm trees and logs, stumps, rotting timber, and sawdust and refuse heaps in which the beetle breeds. The dead palm trees and other logs which attract beetles for egg laying are cut into convenient lengths, allowed to dry, and burned. The contents of refuse and sawdust heaps are burned in simply constructed incinerators. Compost and animal manure heaps are inspected periodically for adult beetles and larvae and any found are destroyed. These control measures are quite generally followed in coconut and oil palm plantations and estates; but, in and around small villages and isolated areas, it is sometimes difficult to enforce these regulations. In such places the injury to palm trees by the beetle is quite noticeable.

During the few weeks in Malaya, I spent a considerable time investigating coconut and oil palm plantations and scattered small plantings of coconut palms around villages and inspecting breeding media for natural enemies of the rhinoceros beetle.

Searches were made for the Scoliid, *Scolia procer* Ill., reported as a parasite of the rhinoceros beetle many years ago by Richards. Only one male adult of this species was found near a coconut plantation. However, in a logged-off clearing in the jungle some distance from the village of Ulu Langat, a number of males and several females were collected. The females were placed individually in breeding containers with *O. rhinoceros* larvae. Although the females lived for some time in these containers they failed to oviposit on the larvae. Scoliid females always sting and immobilize the host larvae before depositing an egg on them. Since this species was found some distance from the natural breeding grounds of the rhinoceros beetle, and it failed to paralyze the beetle larvae or oviposit on them, it seems doubtful that *S. procer* is a parasite of this beetle. It is possible that the larvae which Richards thought to be those of *O. rhinoceros* were those of another Scarabaeid.

The Scoliid wasp, *Scolia ruficeps*, has been reported by Corbett as a possible parasite of *Oryctes*. Investigations in Malaya by Simmonds failed to show that this species was a true parasite of the beetle. However, he states that it is possible that a biological race of this Scoliid may be able to develop on it. This rather small species was encountered occasionally feeding on flowers in or near rubber plantations. Adult females placed with *Oryctes* larvae in breeding containers failed to paralyze or oviposit on them.

Several other medium-sized and large Scoliids including *Campsomeris javana* were collected, brought to the laboratory and placed in breeding containers with beetle larvae of different sizes. In no instance did any of these Scoliids show any interest in the larvae.

A medium-sized Scoliid, determined as *Scolia patricialis* Burm., was observed in considerable abundance in the coconut plantations around the general Klang area. Females which closely resemble *S. procer*, and which were confined with rhinoceros beetle larvae in breeding containers, stung and paralyzed the grubs but did not oviposit on them. It is possible that no eggs were deposited because of improper laboratory rearing technique. Sometimes it is difficult to induce Scoliid females to oviposit on host larvae in laboratory breeding containers. Of the few larvae that could be found in or near the plantation none were found parasitized. However, since adults of this species were observed in considerable numbers in the vicinity of coconut plantations and since the females readily attacked and paralyzed *Oryctes* grubs in breeding containers, it is assumed that *S. patricialis* or a strain of this species is a parasite of the rhinoceros beetle.

The Carabid beetle, *Catoscopus facialis*, has been reported as a predator of *Oryctes* larvae, and before the war adults of this Carabid were successfully introduced into Samoa from Malaya. A search was made for this beetle during the short stay in Malaya, but none was found. Although this predator feeds on the larvae of the rhinoceros beetle as well as of other insects, it is questionable just how effective it is in controlling the beetle.

The green muscardine fungus, *Metarrhizium anisopliae* Metsch., has been reported from many countries in Southeast Asia including Malaya as attacking *Oryctes*. A casual search was made for rhinoceros beetle larvae infected with this fungus in Malaya but none was found. Several investigators have reported varying degrees of success in controlling the beetle with this fungus. Fredericks has described his tests in Samoa with inoculated breeding traps for the control of *Oryctes* as highly successful, whereas other investigators have reported little effective control by this method. It appears that factors which regulate the degree of infection of the larvae in the inoculated breeding compost piles or traps were not recognized in these tests. It is quite possible that these factors are responsible for the differences of results obtained by the several investigators. In connection with this it is interesting to note that Dutky, in investigations with *M. anisopliae* on Japanese beetle larvae, has found that the moisture content of various types of soil and with mixtures of soils with other materials such as sand, talc and charcoal is an important factor in controlling the effectiveness of this fungus. In soil or other moist media at low moisture contents he found that particles adhere to the cuticle of insects whereas at moderate moisture levels the larvae make their way through the medium without adherence of particles. At high moisture levels, the movement of the larvae through the medium puddles it and causes the moist medium to become plastered to the cuticle of the larvae. In soil where the spores are largely bound to the soil particles the free spores will behave in much the same way as other particles, there being no opportunity for infection at moderate moisture content since contact is not maintained between the spores and the cuticle. Thus it is prossible in controlled laboratory tests with soils heavily inoculated with spores (500,000 spores per gram of soil) to obtain at will no infection or substantially 100% infection of exposed larvae by varying the moisture content only a small amount at the critical level. In soils, muck, and similar moist media, the critical moisture content for adherence and infection is related to the ballpoint of the soil or water absorption coefficient. The maximum moisture level at which particles will adhere to the cuticle is about 60% of the ballpoint value. The minimum temperature at which infection was obtained in these experiments was 12 degrees C. The minimum for growth of *Metarrhizium* is below 10 degrees C., while the maximum temperature at which growth could be obtained was from 32 to 34 degrees C. It would be interesting to determine if similar results, based on these findings, could be obtained with *Metarrhizium* on *Oryctes* grubs. If favorable results were obtained they might be applied with success to properly prepared compost heaps and traps infested with larvae of the beetle.

The rhinoceros beetle is present throughout the coconut producing areas in Southeast Asia and further investigations in this general area may reveal other parasites, predators and diseases of this beetle.

SUR LES CALEOPTERES LUCANIDES DES PHILIPPINES NOTE SUR LEUR CHOROLOGIE

Par E. Séguy
Laboratoire d'Entomologie du Muséum
National d'Histoire Naturelle
Paris, France

Près de quarante espèces de Lucanides sont actuellement signalées comme habitant l'Archipel des Philippines. L'ensemble peut se répartir dans douze genres très differents. On sait que les Lucanides du globe forment actuellement plus de cent genres et que la faune européenne de ces insectes est répartie en sept genres, que la faune africaine ne comprend qu'une dizaine de genres, et que, au contraire, Bornéo, Java, Sumatra sont habités par de très nombreuses espèces divisées en vingtcinq genres. On voit déjà par ces exemples que les Philippines possèdent proportionnellement beaucoup plus d'espèces que les autres contrées du globe. Il est intéressant de préciser l'endémicité des Lucanides philippiniens et de rechercher leurs affinités.

La faune des Philippines, relativement homogène, est caractérisée par la rareté des formes de grande taille. Les Chiasognathines, les Lamprimines, les Lucanides manquent absolument. Les Chalcodines sont représentés par deux genres et quatre espèces. L'*Odontolabis fratellus* signalé de Luzon habite aussi Bornéo, mais les *O. intermedius* et *camelus,* et le *Neolucanus alces,* habitent exclusivement les Philippines.

Le *Neolucanus alces* (Fabricious), type du genre *Neolucanus,* est le plus commun. Les différentes formes de ce Chalcodine occupent exclusivement les Iles Philippines. La forme typique est connue de Luzon, la variété *cummingi* (Westw.) paraît localisée aux environs de Manille, la variété *dux* (Westw.) est connue des Philippines sans indication plus précise. La variété *portax* Didier et Séguy représente un intermédiaire entre les exemplaires amphiodontes et prionodontes de la forme typique. Ce *portax,* fourni autrefois à H. Boileau par H. Donckier, porte l'indication de localité "Inde." Cette indication est probablement fausse.

Les Cladognathines comprennent quatre genres philippiniens.

Le *Metopodontus occipitalis* (Westw.), signalé de Luzon, est connu encore de Célèbes, Bornéo, Nias, Sumatra et de la Birmanie méridionale. Les exemplaires philippiniens des collections du Muséum sont beaucoup plus robustes que ceux des contrées voisines. Il n'est pas exclu que des recherches attentives puissent montrer que l'espèce des Philippines est différente. Les localités des échantillons que l'on possède sont trop peu précises pour conclure avec certitude.

Les *Prosopocoelus* sont nombreux. Ceux que sont connus de l'Archipel habitent exclusivement les Philippines, e.g. *cavifrons, dorsalis, ebeninus, lateralis, laterotarsoides, palawanicus* et *vittatus.*

Les trois espèces qui rentrent dans les genres *Cyclommatus* et *Aphanognathus* sont également spéciales aux Philippines. On connaît les *Cyclommatus cupreonitens* et *Zuberi.*

Malgré l'affirmation de Shultze (*Phil. Jl. of Sc.*, XI, 1916, p. 296), l'identité du *Cyclommatus Zuberi* Wat. avec le *C. Fuller-Bakeri* n'est pas certaine. Les caractères de cette dernière forme ont été exactement mis en valeur par Heller (*Ent. Mitt.*, IV, 1915, p. 291). La forme majeure du *C. Fuller-Bakeri* (Arch. Bismarck: Ile Wallis) présente des mandibules armées d'une dent médiane grêle, non épaissie et basale, le clypéus saillant présente un bord antérieur arrondi, non déprimé, le sinciput est moins creusé. Les petits mâles et les femelles sont cependant difficiles à séparer dans les deux espèces (Didier et Séguy, Catal., p. 60, note 106).

Le genre montypique *Aphanognathus*, avec l'espèce *minutigranosus*, est propre aux Iles Philippines. La localité exacte n'est malheureusement pas précisée et l'insecte n'a pas été re trouvé depuis la description de Heller en 1927. L'*A. minutigranosus* se place entre les genres africains *Homoderus et Homoderinus* et près des *Auxicerus* néotropicaux, sans que l'on puisse déceler de relations phylogénétiques entre ces différents genres.

Parmi les Dorcines, l'*Eurytrachellus cribriceps* Chevrolat, une petite espèce spéciale aux Philippines, est remarquable par sa delicate couleur châtaigne. Au contraire, l'*Eurythrachellus Titanus* et sa variété *Typhon*, spéciale à Luzon et à Célèbes, sont des espèces gigantesques d'un noir brillant. C'est le plus grand des Lucanides de l'Archipel. Il peut atteindre plus de millimètres. L'*E. Titanus* est répandu dans toute la région orientale. Le Japon en possède une forme moyenne.

Les Dorcides comprennent assi les petites espèces du groupe *Gnaphaloryx-Xenostomus.* Deux espèces de *Gnaphaloryx* sont spéciales à Luzon et à Mindanao. Le *Metaliactulus parvulus* habite les environs de Manille et Formose. Quatre *Aegus* sont spéciaux exclusivement aux Philippines. Il faut y ajouter l'*Aegus chelifer*, commun et répandu dans toute la région orientale.

Le genre *Xenostomus* Boileau comprend trois espèces. Une, *insolitus* Jak., décrite de Mindoro-Mindanao, et deux autres très différentes de Bornéo, *Krieschei* Nagel et *punctipennis* Parry. Les *Xenostomus* appartiennent à un groupe d'espèces dont les représentants habitent l'Asie orientale et la région guinéenne.

Les petits Lucanides de la sous-famille des Figulines renferment cinq espèces de *Nigidius* dont les *N. Fruhstorferi* et *Lichtensteini* se retrouvent à Java et à Célèbes, les trois autres ne sont connues que de l'Archipel philippinien; trois *Figulus*, dont le *fissicollis* Fairmaire, sont répandus dans toute la région australienne.

Deux *Diasomus* spèciaux aux Philippines appartiennent à cette sous-famille, les *D. cribratus* et *laevigatus*. La localité n'est pas précisée pour ces deux espèces. L'identité du *D. laevigatus* Deyrolle et du *Cardanus tamburan*, décidée par G. Arrow (*Ann. Mag. N.H.*, 1938, p. 52) n'est pas certaine. Cette dernière espèce habite la Nouvelle-Guinée et les Moluques.

Les Syndésines, Aesalines et Sinodendronines ne sont pas représentés aux Philippines.

En résumé, la faune lucanidienne des Philippines, d'après ce qui précède, comprend 37 espèces. 27 espèces, caractéristiques des Philippines, ne sont connues que de cette région. Elles se répartissent comme il suit: 3 Chalcodines, 10 Cladognathines, 8 Dorcines, 6 Figulines. Dix espèces ubiquistes habitent les Philippines et les pays voisins; parmi celles-ci trois formes; le *Metopodontus occipitalis*, l'*Eurytrachellus Titanus* et l'*Aegus chelifer* sont répandus dans toute da région orientale. Une autre, le *Figulus fissicollis*, est spéciale à la région australienne. Géographiquement, les différents Lucanes philippiniens se laissent répartir comme il suit d'après les localités connues des auteurs.

15 espèces sont citées de l'Archipel sans autre précision: 2 Chalcodines, 6 Cladognathines, 6 Dorcines, 1 Figuline.

14 espèces sont connues de Luzon: 2 Chalcodines, 3 Cladognathines, 3 Dorcines, 6 Figulines.

3 espèces de Mindoro appartinnent à trois sous-familles différentes: Cladognathines, Dorcines, Figulines.

Une espèce de Cebu (Chalcodine).

3 espèces de Mindanao se classent dans les Cladognathines, Dorcines, Figulines.

Une espèce de Palawan (Chalcodine).

Conclusion.—Les connaissances fragmentaires que l'on possede sur la faune lucanidienne de Mindoro, Cebu, Mindanao et Palawan ne permettent pas de conclure définitivement. Mais les grandes collections du Muséum de Paris fournissent une documentation suffisante pour affirmer que les Iles Philippines possèdent une faune endémique importante représentant près des deux tiers de la population spécifique totale (comme 27/10). Quatre espèces seulement sont ubiquistes, plusieurs autres pourront être incorporées au contingent endémique lorsque nos connaissances sur les espèces douteuses auront été perfectionnées. Aucun groupe d'îles sur le globe ne possède une endémicité lucanidienne comparable à celle des Iles Philippines. L'isolement spécifique a certainement joué ici un rôle important.

La région sud-orientale, particulièrement riche en Lucanides, semble bien, suivant Leuthner (Monogr., p. 482) représenter le centre de dispersion des éléments de cette famille. La sous-région philippinienne (qui fait partie de la région orientale) a peut-être servi de refuge à certaines espèces qui ont évolué sur place—ou les Philippines représentent un centre de dispersion au même titre que Sumatra, Java ou Bornéo par exemple. L'absence de documents paléontologiques ne permet pas de choisir entre ces deux hypotheses.

Des récoltes massives d'insectes, dans des localités exactement précisées, avec l'indication du biotope, permettront l'étude généalogique des représentants de la famille des Lucanides.

Les études systématiques n'ont pas seulement pour but de faire connaître les espèces nouvelles, mais encore d'esquisser la phylogénie des formes connues et de mettre en évidence les unités biogéographiques qui formeront des lignées homogenes.

November 20, 1953

Presiding: Dr. M. A. Lieftinck, Director, Museum Zoologicum Bogoriense, Bogor, Indonesia.
Secretary: Dr. Silverio M. Cendaña, College of Agriculture, University of the Philippines, College, Laguna.

. . . .

PROCEEDINGS

1. Dr. Lieftinck read the report of Dr. E. G. Turbott, Chairman of the Standing Committee on Distribution of Terrestrial Faunas of the Inner Pacific, in the absence of Dr. Turbott.

   There was a short discussion after the reading of the paper:

   Dr. Pemberton: The scope of the paper is very broad. It is suggested that separates of the paper be sent to the Central Headquarters of the Pacific Science Board for compilation.

   Dr. van Steenburgh: He reiterated the points brought out by Dr. Pemberton.

2. Britton, E. B. Insect Distribution and the Theory of Continental Drift.

   Only the title of the paper was read, since Dr. Britton failed to come. A copy of his paper had been received after the Congress sessions.

3. Vachon, Max. Remarques sur la Repartition des Scorpions en Oceanie.

   Only the title of the paper was read, since the author failed to attend the Congress and no paper had been received from him.

4. Cain, A. J. Range-changes and Differential Selection in Fruit Pigeons of the *Ptilinopus purpuratus* Species-group. (Abstract on page 28 of Supplement of Abstracts of Papers.)

   The author failed to attend the Congress so the abstract of his paper was read.

5. Otanes, Faustino Q. Entomological and Plant Pest and Disease Control Work in the Philippines with Special Reference to that of the Bureau of Plant Industry on the Migratory Locust and other Major Pests and Diseases of Crops. (Abstract on page 121 of Abstracts of Papers.)

There was much discussion after the reading of the paper by the author. Part of it follows:

Mr. Rabor: What were the birds shown in the picture (passed around)?

Mr. Otanes: They were not birds—they were locusts.

Dean Uichanco: I would like to correct the impression that might have been formed about swarming. Locust swarming may occur anywhere but these are not necessarily the permanent breeding places.

Dr. Townes: They might be interested in that map. (Mr. Otanes showed the location of locust swarms on the map of the Island of Burias.)

Dean Uichanco: The subject (of locust breeding area and swarming) is complicated.

Mr. Otanes: For that reason we are recommending the establishment of a locust laboratory in Cotabato.

Dr. Cendaña: In one of the lots of locust nymphs purportedly from Burias, we reared a tachinid fly. Did you happen to notice many of these tachinid parasites on locust?

Mr. Otanes: Yes. Also egg parasites.

Dr. Bess: What is the extent?

Mr. Otanes: By the time the swarms have been thinned, they are relatively more.

6. Pangga, Guillermo A. Further Studies on the Biology, Ecology and Control of the Giant East African Snail (*Achatina fulica* Fer.) (Abstract on page 137 of Abstract of Papers.)

There was a good discussion on the snail after it was read by the author. Part of it follows:

Dr. Bess: (Spoke about the efforts in Hawaii and the Marianas to control the snail by introducing a meloid beetle and a small predatory snail from East Africa.) The predatory snail seems to be of great promise, although it does not seem to kill beyond 12 per cent of giant snail. It is still under study.

Dean Uichanco: It might be desirable if the predatory snail is introduced in the Philippines. (To which Dr. Bess assured cooperation from Hawaii.)

Dr. Bess: How much has the snail spread in areas where they were found?

Dean Uichanco: In fairly moist places such as along river beds and in the vicinity of water.

Dr. Lieftinck: How effective is the metaldehyde?

Dr. Owen: The metaldehyde seems to lose its efficiency after a few days.

Dr. Cendaña: If used with some ripe fruits, such as papaya, nangka and even peelings of apple, the bait becomes more attractive to the snail and is very efficient. By dishing it out on peelings of ripe papaya, and brushing the dead snails off the bait every morning, I killed 36,000 snails, by actual count, with 1 kilogram of the bait. The bait is no longer attractive after 3 nights of exposure.

7. Gressitt, J. L. The Insect Fauna of Micronesia. (Abstract on page 139 of Abstract of Papers.)

Some lantern slides were shown after the paper was read, showing some of the habitats in some of the islands where collections have been made.

Part of the discussions after the reading of the paper follows:

Dr. van Steenburgh: What type of vegetation are those in top of the ridges?

Dr. Gressitt: Looks like they were ferns.

Dr. Townes: Some of the islands are a few inches high (from the surface of the ocean). At times they become submerged so that most insects on them die, although there are many Pandanus which could possibly maintain some insect life. The insects are mostly introduced. In the higher islands the conditions are slightly different.

Dr. Pipkin: On. (one island) there are 2 or 3 species of mosquitoes. On Truk Island there are also a few species of mosquitoes.

Mr. Otanes: Were they carried by wind? How are their chances of survival?

Dean Uichanco: By typhoons, possibly?

Dr. Gressitt: Some insects of the lowland are found at top of mountains after typhoon.

Dr. Lieftinck: Do we understand that you are putting out a series of these papers?

Dr. Gressitt: We are putting out the Introduction. The others will follow but will possibly be long delayed.

8. Kondo, Yoshio. Status of Terrestrial Malacological Research in the Central Pacific and Micronesia. (No Abstract.)

In the absence of the author, the paper was read by Mr. Rabor. It was pointed out in the paper that:

(a) There are certain species that are indigenous to the Pacific and not found elsewhere.

(b) There are two phases in the work (1) studies in the field, and (2) studies in the laboratory.

(c) A list of islands from which collections have been made and published on was included.

9. Powell, A. W. B. Land Molluscan Distribution in the Southwest Pacific. (No Abstract.)

The paper was read by the author. It concerned mainly the distribution of land molluscs in the Central Pacific. The author referred to four earlier publications of his (1947–1952) in Auckland.

There was a short discussion on the paper.

10. Manuel, Canuto G. Status of Tamaraw. *Anoa mindorensis* (Heude). (Abstract on page 29 of Supplement to Abstracts of Papers.)

A lively discussion followed the reading of the paper by the author.

11. Gardner, Theodore R. Collection and Distribution of Beneficial Insects in the Pacific Area and Southeast Asia. (See Abstract on page 23 of Supplement to Abstracts of Papers.)

The paper was read by the author. There was a short discussion on the paper.

12 Brown, Walter C. The Distribution of Terrestrial Reptiles in the Islands of the Pacific Basin.

(The paper was submitted after the Congress sessions.)

INSECT DISTRIBUTION AND THE THEORY OF CONTINENTAL DRIFT

By E. B. Britton
British Museum (Natural History)
London

The author is of the opinion that the hypothesis of continental displacement receives less attention from biologists than it deserves. The reality or otherwise of drift must have a basic influence on our ideas on the causes of the observed distribution of animals and for this reason the search for evidence for and against the hypothesis should be a major concern of zoogeographers. There is a tendency among biologists to regard this as an exclusively geological problem. Geologists are inclined to reserve judgment on the subject while geophysicists reject the theory on the ground that it cannot be explained, and as a result the problem is shelved.

The present paper is an attempt to present very briefly, as a basis for discussion, an analysis of the indications provided by the observed distribution of insects.

The main problem presented by the present geographical distribution of insects is that of discontinuity on the continental scale. We want to know why the distribution of so many groups of insects is so completely at variance with the present distribution of land. When closely related species are found in different continents it is obvious that some kind of link between the continents must have existed in the past. Assuming the systematics to be sound, the species in the two or more continents must have had a common ancestor which in some way passed from one continent to the other.

Two kinds of links are possible. The first is accidental transference of individuals from one part of their present range to another, by floating débris in the sea, by high winds, or on birds. If the connection was not due to such accidents then it must have been by way of a more or less continuous land link.

The relationships between the members of the group must be real and not due to convergence, or the results will be meaningless.

There can be no disputing the view that a distribution such as this indicates some sort of link between the various locations in the past. The ancestors of the Aepini in some way got to all these places.

What sort of links are possible? There are two kinds. First the link may be due to accidental transference of individuals from one part of the range to another, by floating débris in the sea, by high winds, or on birds. If the connection was not due to such accidents, then it must have been by way of a more or less continuous land link.

Now let us consider the possible importance of the accidental transport of insects. Obviously this does happen. The question is whether it is sufficiently frequent and effective to account for the observed patterns of distribution.

The insect fauna of the Hawaiian Islands is instructive in this connection. These islands are entirely volcanic and have therefore received the whole of their pre-human fauna as the result of chance introduction. The islands appear to be not older than late Pliocene, and Zimmerman has demonstrated that the whole of the insect fauna of about 4000 species has resulted from not more than 260 separate introductions. That is, there have been only 260 successful immigrants in 2 or 3 million years. Nevertheless, if some insects have reached, by accident, these relatively minute specks of land, whether directly or by a process of "island hopping," then insects may also cross oceans such as the Atlantic with greater frequency, because the target is so much larger.

It must be remembered, however, that the chances of survival of an immigrant were probably much greater in the Hawaiian Islands than on a continent owing to the simpler environment and the relative absence of predators.

Clearly the successful transfer of insects from one continent to another across the sea must be rare but can happen, but a further study of the Hawaiian fauna shows that the transfer is limited to certain kinds of insects only. It is significant that among the Hawaiian insects, in spite of the abundance of streams, there are no insects with aquatic larvae, with the exception of Dragonflies, the adults of which are well known for their strong flight. The highly selective nature of the fauna is also shown by the fact that the great majority of the Hawaiian Coleoptera are wood feeders or tree dwellers. At a conservative estimate there are 140 families of Coleoptera in the world. Of these only 19 occur in the Hawaiian Islands.

Clearly the majority of insects do not lend themselves to accidental transport by sea or air. But it may be argued that however small the chance of a successful accidental transfer of an insect from one continent to another, it may be appreciable when multiplied by time on the geological scale. Given time the seemingly impossible may happen.

To decide this question we need an insect whose living requirements are so restricted that we can be certain that its accidental transport is impossible. The Peloridiidae are insects of this sort.

The Peloridiidae are a family of Hemiptera—Homoptera including 8 species in 3 genera. The great phylogenetic importance of this small family is shown by the fact that it forms a special series of the Homoptera, the Coelorrhyncha, equivalent to the Auchenorrhyncha which includes the Cicadas, Leaf Hoppers, Frog Hoppers and Membracids, and to the Sternorrhyncha which includes the Aphids, Psyllids, Aleurodids and Coccids.

The Peloridiids are in fact the most primitive living Hemiptera. These insects are about 3 mm. long. They lack hind wings and so are unable to fly. Even the forewings are more or less reduced. Most interesting of all, the Peloridiids are the only living insects with lateral flaps on the pronotum which are almost certainly homologous with wings.

Peloridiids are found in moss on the floor of the Antarctic Beech forest in Patagonia, New Zealand and Eastern Australia. Figure 1 illustrates specimens from each of these localities. Figure 2 is a South Polar Projection showing the distribution of Peloridiidae.

These insects move very slowly and feign death if disturbed. They never appear on the surface of the moss which is their food plant unless rain is actually falling, or the humidity is close to saturation. The moss in these cold rain forests is permanently saturated.

All who have collected or studied these insects consider it impossible that their ancestors could have been transported alive across the 2000 miles of ocean between Australia and New Zealand, quite apart from the further 4500 miles to Patagonia.

That the Peloridiids could not have been transported by chance is emphasized by the fact that a very successful group of insects, the Aphids, which are winged and notorious for the ease with which they are carried by air currents, did not reach Australia or New Zealand until the arrival of Europeans. Similarly there are no native Thysanoptera in New Zealand, although they are abundant in Australia and are known to be carried by wind. Both Aphids and Thysanoptera are far more resistant to changes of environment than the Peloridiids, so that if they cannot cross the ocean it seems certain that the Peloridiids could not do so.

Here I would point out that the investigation of the environmental tolerance of Peloridiids offers an interesting line of research. It is probable that these insects are not nearly so uncommon as is suggested by the few specimens in collections. With a little experience a careful collector could probably obtain enough living specimens for experiments on humidity, temperature and sea water tolerance. The results of such a study might go a long way to confirm the opinion that Peloridiids could not cross an ocean. It could be argued that the common ancestor of present day Peloridiids might have had less restricted tolerances. The existing forms are, however, so closely related and similar in habitat that this seems most unlikely.

We may conclude that some discontinuous patterns of distribution at least are not explainable by chance introduction across an ocean barrier but need some more or less continuous land connection. And if an intercontinental land connection is demonstrated for even one group, then we are at liberty to explain the hundreds of other similar distributions in the same way.

Assuming that we accept the existence of some sort of land connection between Australia, New Zealand and Patagonia we may now inquire into the nature of this connection. There are three possibilities.

The first is that Australia, New Zealand and Patagonia were once connected by a land bridge, a former continental extension across what is now deep ocean. Such a connection would probably have included Antarctica when the climate of that continent was less extreme. Even if this were the case, there are still 1500 miles of deep ocean between Tasmania and Antarctica to be bridged.

Now I assume that in geology the principle of isostasy is accepted. This means that the continents are in a state of hydrostatic equilibrium with relation to the underlying layers. In a general way they may be said to float. If isostasy is a fact it would be impossible for a large continental mass to be depressed to oceanic depths or to remain submerged. When we think of raising or sinking bridging continents, it must be remembered that there are on earth two markedly favoured levels, the surface of the continents with an average height of 2700 ft. above sea level, and the floors of the oceans with an average depth of 12500 ft. The oceans on the average are five times as deep as the land is high. Between the two is the continental shelf, a very constant and striking feature. These are remarkable facts. They indicate that the continental surface and the true deep ocean floor are not interchangeable.

Again I understand it is a fact that none of the deposits which are characteristic of the deep ocean floors are found on the surface of the continents. This suggests that if there have been transoceanic land bridges in the past, then they must all be sunk without trace at the present time, which would be a singular coincidence. The sort of land bridge that does exist today is illustrated by the isthmus of Panama.

The isthmus certainly has been submerged in the past, but no one suggests that it was covered by any more than a shallow sea.

It appears that while zoologists would be satisfied with bridging continents, there is a complete lack of geological evidence in favour of such bridges, and an accepted geological principle even denies their possibility.

If we conclude that there have been no bridging lands between the continents, two possibilities remain. The first is the theory of radial distribution from the northern hemisphere, which was developed by Matthew in 1915.* The second possibility is continental drift. Both assume the relative permanence of the total area of the continental masses, but the radial theory assumes that the relative positions of the continents have also been permanent. The radial theory also demands periodic world-wide changes of climate which both caused the movements of faunas and followed them to pass the tropics. Here the links between the continents are in the northern hemisphere, around the north pole. These connections are of course virtually in existence today, for a very small fall in sea level would produce continuous dry land around the pole. It is not doubted, of course, that transfers of fauna have occurred between Europe and North America, and more recently, between Northern Asia and North America across what is now the Bering Strait. These transfers have been possible so recently that we find species encircling the Arctic today. The theory was built by Matthew mainly on the past and present distribution of Mammals, and this is undoubtedly the true explanation of many mammalian distributions. Much use was made by Matthew of the North polar projection which emphasizes the unity of the northern hemisphere, but gives an entirely false view of the relations of the southern continents.

The relations between the faunas of southern South America, Australia and New Zealand are so many and so close that it is difficult to believe that the only links between them are by way of two continents and an Arctic link. As an example of the closeness of these links we can take some representatives of the Blephariceridae, a family of Diptera. Blepharocerid larvae are strictly confined to waterfalls and broken water in mountain torrents. The specimens in Figure 3 are two species of the same genus, *Edwardsina tillyardi* from New South Wales, and *Edwardsina gracilis,* from Patagonia.

If Matthew was right then *Edwardsina* must have spread from some unknown source down two continents, or up one continent and down another, without diverging to more than specific level. And the spread adults fly, they do so only feebly, and their spread must be limited to mountain areas which alone produce the right kinds of streams.

---

* Matthew, W. D. 1915. "Climate and Evolution," *Ann. N. Y. Acad. Sci.* 24: 171-318.

The Peloridiidae, considered earlier, provide a similar example. They are restricted to the cool rain forests of the southern hemisphere, and it is impossible to believe that these sluggish wingless creatures could have migrated through two continents, still retaining the very special ecological conditions to which they are adapted.

The usual answer to arguments against migrations of this kind is that the fauna was once world wide or was at least very extensive, and that what we see now are relicts. This may be legitimate in the case, say, of the Marsupials but it is not possible to imagine a world wide fauna of Peloridiids.

Examples of this kind lead to the conclusion that while Matthew's theory may explain much of the more recent distribution of the Mammals, it entirely fails to account for the close links between the southern continents.

We turn lastly to the Drift theory, which has the advantage to the biologist of explaining both the northern and the southern links. Like the radial theory it assumes that the total continental area has remained more or less constant, and differs in assuming that the continents were once assembled in one continuous mass. It assumes that the continents not only float on the denser layers beneath, but that these lower layers are, or have been, plastic, so that the continents are able to move laterally. The originally continuous Pangaea is assumed by Wegener to have started to break up in the early Jurassic, with a fissure separating what is now Australia, including New Guinea and New Zealand, from Asia. This fissure widened and progressed around Africa opening up the Atlantic in the Cretaceous. The main direction of drift is assumed to have been westward, that is, in the direction opposite to the earth's rotation. South America, Antarctica and Australia are assumed to have remained in contact up to Miocene times, which serves to explain the close faunal links between Australia and Patagonia.

If Africa was separated from the South American-Australian mass in the early Cretaceous, we should expect to find the relations between the faunas of S. Africa and Australia less close than those between Australia and southern South America, and that these similarities would be restricted to the more primitive groups. This is so, for example, in the stone-flies of the sub-family Notonemourinae. The sub-family includes two genera and five species from Australia, Tasmania and New Zealand, and four genera and seventeen species from Cape Province, and others from southern South America.

To summarize very briefly, I suggest that we cannot accept distribution by wind or sea as more than a subsidiary cause of the distribution of insects, so that there must have been land connections between the continents in the past. There are three possible ways by which the land connections could have been achieved. First by bridging continents now sunk to oceanic depths. Second by way of the existing arctic connections. Third by assuming a single original continental mass, subsequently broken up by continental drift.

I believe that we are forced to reject oceanic bridges on geophysical grounds and because no traces of such bridges remain. The radial theory must be rejected on biological evidence from the southern continents. We are left with Drift, which explains the biological facts. I know of no biological evidence which contradicts Drift and the most that its biological opponents can say is that it is unnecessary.

The one strong argument against Drift is geophysical. It is claimed that no forces exist which are sufficient to move the continents. I cannot believe, however, that this is sufficient justification for discarding the theory. As in the case of Evolution itself, theory is built on observation, and explanation of the mechanism comes later.

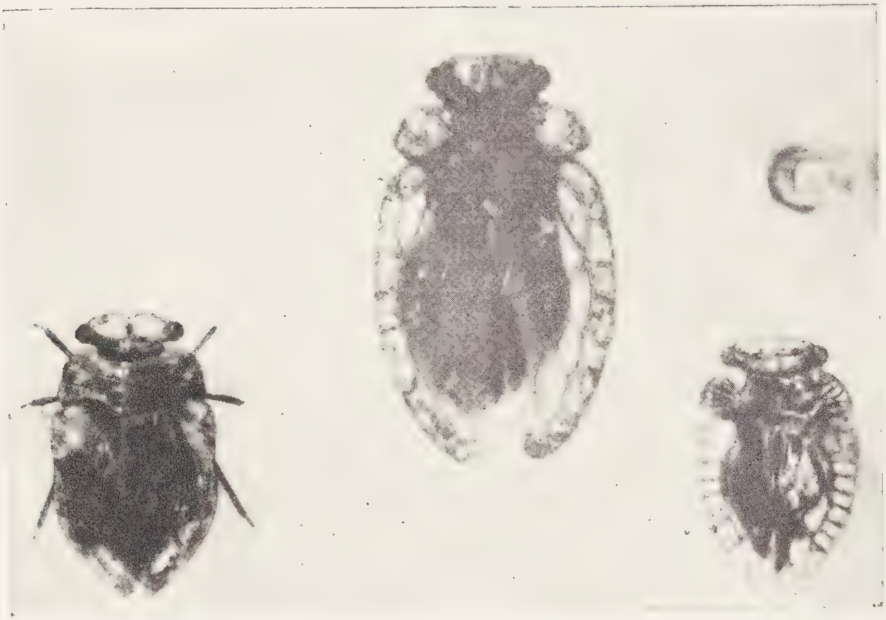


FIG. 1.—Examples of Peloridiidae:

left: *Hemicdoecus leai* (Tasmania).
middle: *Peloridium hammoniorum* (Patagonia).
right: *Xenophyes cascus* (New Zealand).

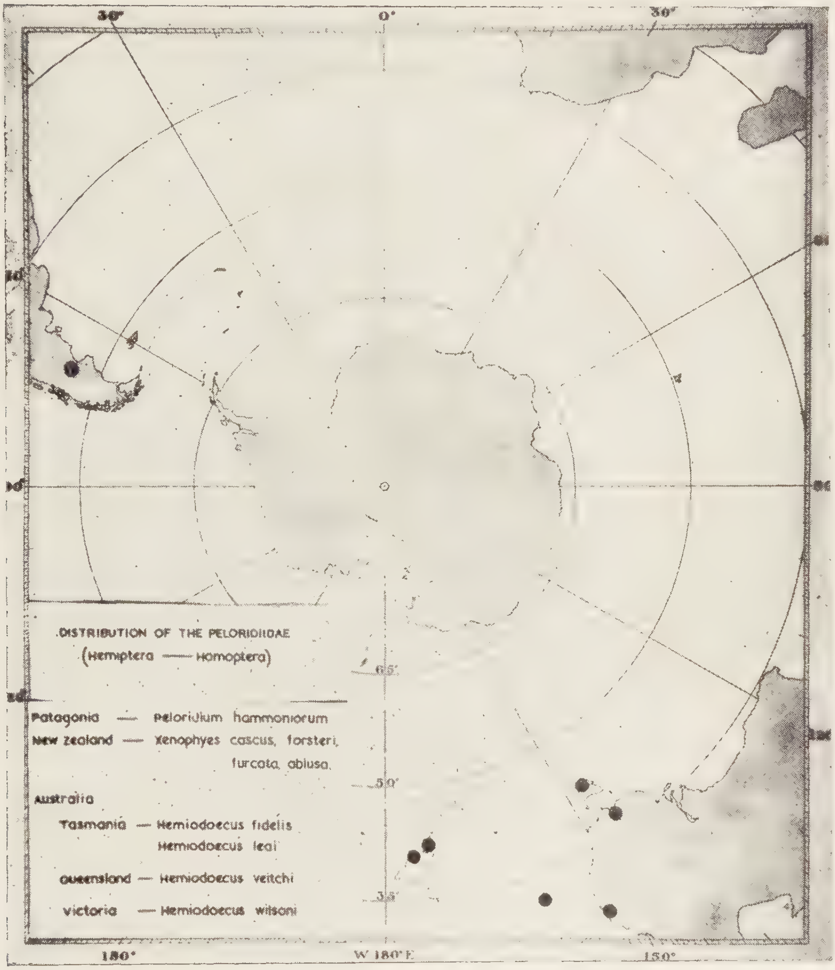

30°
0°
30°
DISTRIBUTION OF THE PELORIDIIDAE
(Hemiptera — Homoptera)
Patagonia — Peloridium hammoniorum
New Zealand — Xenophyes cascus, forsteri, furcata, oblusa.
Australia
Tasmania — Hemiodoecus fidelis
Hemiodoecus leai
Queensland — Hemiodoecus veitchi
Victoria — Hemiodoecus wilsoni
65°
50°
35°
180°
W 180° E
150°

FIG. 2.—Distribution of Peloridiidae.

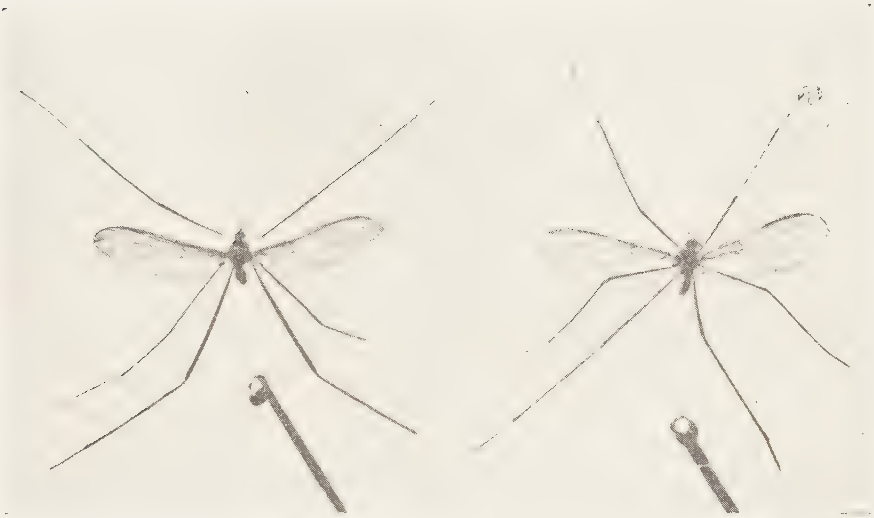


FIG. 3.—Examples of Blepharoceridae:

left: *Edwardsina tillyardi* (New South Wales),
right: *Edwardsina gracilis* (Patagonia).

REMARQUES SUR LA REPARTITION DES SCORPIONS EN OCEANIE

Par Max Vachon
Muséum National d'Histoire Naturelle
Paris, France

RANGE-CHANGES AND DIFFERENTIAL SELECTION IN FRUIT-PIGEONS OF THE *PTILINOPUS PURPURATUS* SPECIES-GROUP

By A. J. Cain
Department of Zoology and Comparative Anatomy
University Museum, Oxford, England

Introduction

The fruit-pigeons of the *Ptilinopus purpuratus* species-group comprise about 40 named forms, mostly geographical representatives, which are distributed from the Marianas and Palau Islands to the Lesser Sunda Isles, Australia, and the archipelagoes east of them as far as the Marquesas, Tuamotus and Henderson Islands. The distributional history is rather complex, including several enormous expansions and multiple invasions. As a result, there are some forms which coexist with close relatives, while others are isolated. The isolated ones may be on large islands (or large archipelagoes of small islands), on small islands near to large ones, or on small islands far from others. It is to be expected that natural selection would act in different ways under these very different circumstances. The forms which overlap with close relatives may be expected to retain or even accentuate complex colour-patterns, while isolated ones should tend to simplify their patterns but at different rates according to their circumstances. Those on large islands or large archipelagoes of small islands may be expected to lose their complex patterns rather quickly since they are represented by large populations and probably have a high genetic variability for selection to work on. Those on small islands moderately near to large ones (or large archipelagoes) should show even quicker evolutionary change, since their variability can be frequently replenished by immigration while the uniformity of their habitats will allow selection to act rather constantly in one direction. Forms isolated on remote small islands, on the contrary, will change very slowly since they will suffer from considerable inbreeding and consequently will be able to maintain very little genetic variability for selection to work on.

All these possibilities are very well exemplified by these fruit-pigeons, and all must be taken into account before a satisfactory distributional history and classification can be produced. The purpose of this paper is to attempt the construction of a distributional history in which such considerations are given their due weight.

I am greatly indebted to Mr. J. D. Macdonald, of the British Museum (Natural History), who has given me every facility for working over the collections under his care.

CHECKLIST

For the reader's convenience a checklist of all the species under consideration is inserted here. Full references to the subspecies will be found in Peters (1937) and Ripley and Birckhead (1942). The justification of the arrangement of species used here is given in the discussions later and summarized in the section on classification (p. 1407).

PURPURATUS SPECIES-GROUP

(i) *Superbus subgroup* (one superspecies).

Pt. superbus (Temminck 1810). Celebes and the Sulu Archipelago; Moluccas; Western Papuan Islands; Numfor and Japen; Aru Isles; New Guinea; Karkar and Manam; D'Entrecasteaux and Louisiade Archipelagos; Admiralty Isles and Bismarck Archipelago; Solomon Islands; islands of Torres Straits; and Australia (Cape York to New South Wales).

Pt. perousii (Peale 1848). Fiji, Tonga, and Samoa.

(ii) *Purpuratus subgroup* (one superspecies plus two doublets, see p. 1408).

Pt. monacha (Temminck 1824). North Moluccas (Halmahera, Ternate Batjan).

Pt. coronulatus (G. R. Gray 1858). New Guinea, Japen, Salawati, and Aru Isles.

Pt. pulchellus (Temminck 1835). New Guinea and Western Papuan Islands.

Pt. regina Swainson 1825. Eastern and northern Australia, eastern Lesser Sunda Isles, Banda and Kei Isles.

Pt. roseicapilla Lesson 1831. Marianas.

Pt. greyii Bonaparte 1857. New Caledonia to Santa Cruz Islands and Gower I.
Pt. richardsii (Ramsay 1882). Ugi, Santa Anna, and Rennell I. (Solomons).
Pt. porphyraceus (Temminck 1821). Fiji, Tonga, Samoa, Caroline and Palau Islands.
Pt. rarotongensis Hartlaub and Finsch 1871. Rarotonga.
Pt. huttoni (Finsch 1874). Rapa I.
Pt. purpuratus (Gmelin 1789). Society Isles, and Tuamotu (or Lau) Archipelago.
Pt. dupetithouarsii (Neboux 1840). Marquesas, widespread.
Pt. mercieri (Des Murs and Prévost 1849). Nukuhiva and Hivaoa (Marquesas).
Pt. insularis (North 1908). Henderson Island.

Reasons for the inclusion of *Pt. superbus* and *Pt. pulchellus* in the species-group, and for the association of *Pt. perousii* with *Pt. superbus* instead of with the purpuratus subgroup have been given by Cain (1953). It is this subgroup that will be principally discussed in this paper.

Effects of Divergent Selection

(i) *Forms coexisting with close relatives.*

Lack (1947) has pointed out that one reason for the plain colouration of birds of oceanic islands is that each lives together with only a few other species, and therefore does not require complex recognition marks and other special visual signals. It is to be expected, therefore, that those species which do coexist with very close relatives should differ from them in song, courtship behaviour, or colour pattern, or any combination of these. This consequence has been beautifully exemplified by Vaurie (1950, 1951) who shows that where the two closely related nuthatches *Sitta tephronota* and *S. neumayr* overlap, they differ strongly not only in body size and beak size but also in the colour pattern of the head, while where they do not overlap they are so similar that there has been considerable confusion over their taxonomic status in the past. It is therefore reasonable to expect that isolated forms of the purpuratus subgroup should show a degenerate and simplified colour pattern, while those that overlap should show complex but different patterns. Such an expectation is in complete accord with the results of Lorenz and Tinbergen (e.g., Tinbergen 1948, 1951), obtained by analysis of behaviour-patterns in relation to visual signals. There is little doubt that as Ripley and Birckhead (1942) have concluded, the centre of origin of the subgroup is in New Guinea. The five most highly ornamented forms are *Pt. monacha* (North Moluccas), *Pt. coronulatus* and *pulchellus* (New Guinea), *Pt. regina* (Australia and the eastern Lesser very closely related to *Pt. coronulatus. Pt. roseicapilla* is extraordinarily Sunda Isles) and *Pt. roseicapilla* (Marianas). Of these, *Pt. monacha* is like the eastern Australian *Pt. regina,* and these two are probably allied rather more closely to *Pt. coronulatus* than to *Pt. pulchellus.* Ripley and Birckhead do not discuss the interrelationships of these forms except to comment on the extraordinary similarity and enormous geographical separation of *Pt. regina* and *roseicapilla.* They omit *Pt. pulchellus* altogether from their treatment of these forms.

It is quite unnecessary to assume that *Pt. roseicapilla* is directly related to the eastern Australian populations of *Pt. regina.* The northwestern subspecies of *Pt. regina* are the nearest to it geographically, and resemble it least. A far more reasonable hypothesis is that the common ancestor was in the New Guinea region and invaded the Marianas to the north and Australia to the South, producing these two species. A fuller discussion of *Pt. roseicapilla* is given later (p. 1401). However, New Guinea is now occupied by both *Pt. coronulatus* and *Pt. pulchellus,* which are almost entirely sympatric. It is known (Carey, 1938) that New Guinea in the past has been split up into two or more islands. This would allow for geographical speciation to take place, the common ancestor giving rise to both *Pt. coronulatus* and *Pt. pulchellus.* Since *Pt. monacha* of the North Moluccas is closely related to *Pt. coronulatus* it is reasonable to believe that the latter was produced on that portion of New Guinea which formed an island near the North Moluccas, while *Pt. pulchellus* appeared on a different portion. (If the differences between *Pt. pulchellus* and *Pt. coronulatus* were accentuated after they met (when the islands joined up), then it is possible that *Pt. roseicapilla* and *Pt. regina* were produced some little while after they met and before their distinctive characters were fully developed.) This distributional history is shown in Figure 1. *Pt. coronulatus* and *Pt. pulchellus* can therefore be considered here as a pair of closely related forms which coexist.

The closest relative of *Pt. regina* is certainly *Pt. greyii* in the New Hebrides. Next is *Pt. porphyraceus* which is centered on Fiji, but, as Ripley and Birckhead point out, has expanded its range enormously to the north and west, producing populations still only subspecifically distinct in the Carolines and Palaus. There has obviously been an enormous general expansion eastward from *Pt. regina,* which itself has expanded northwestward, producing subspecies in the Banda Sea region. The forms even further east have also been produced from the Australasian stock, but their history requires further discussion (p. 1405). At all events, it is certain that the Marquesas have been invaded twice from the west, by a single stock, producing the two Marquesan species, *Pt. mercieri* and *Pt. dupetithouarsii.* These and the two New Guinea forms, *Pt. coronulatus* and *Pt. pulchellus,* provide in this group the examples of forms coexisting with close relatives.

A comparison of the similarities and differences between *Pt. pulchellus* and *coronulatus* on the one hand, and *Pt. mercieri* and *dupetithouarsii* on the other, shows clearly that the members of each pair are more closely related to each other than to either member of the other pair (Fig. 2). *Pt. pulchellus* and *coronulatus* agree closely in the rich deep green of the back and wings, the virtual absence of dark scapular spots (which are conspicuous and well-defined in *Pt. superbus, roseicapilla* and *regina*), the comparative scarcity of rather narrow, clearly bifid breast-feathers (abundant and very well-marked in these three other species) and the presence of a well-marked richly coloured abdominal band (*Pt. pulchellus*) or spot (*Pt. coronulatus*), in which these two species agree with all the western forms of the purpuratus group. Both are rather small (winglength about 115 mm.), being the smallest *Ptilinopus* in New Guinea, excepting only *Pt. naina* (hyogastra species group). They are birds of the lowland forest, (Mayr 1941), small, and obviously protectively coloured above. *Pt. dupetithouarsii* and *mercieri* are both rather large (winglength about 145 mm.). Both have extensive dark blue spots on the wing coverts, the yellow edges of which are rather wide, and in both the back is, comparatively, rather pale green, not rich deep green as in the western pair. Neither has any trace of an abdominal spot or band, but both have a large abdominal patch, yellow (*Pt. mercieri*) or orange (*Pt. dupetithouarsii*). In the absence of an abdominal spot they agree with their neighbours *Pt. purpuratus* and *insularis,* and partly with *Pt. rarotongensis* in which the spot is very small.

In both pairs one member has a bright red cap (*Pt. pulchellus, mercieri*) while in the other it is much paler (lilac in *Pt. coronulatus,* white in *Pt. dupetithouarsii*). In the same member of both pairs the breast is sharply marked off from the abdomen (*Pt. pulchellus, Pt. mercieri*) while in the other there is a rather small rounded abdominal spot (*Pt. coronulatus*) or patch (*Pt. dupetithouarsii*) around the sides of which there is a gentle gradation from the colour of the breast to that of the flanks. In both, when the abdominal ornament is well-defined, it is also of a brighter hue (bright yellow in *Pt. mercieri* as against dull orange and dull grey-green in *Pt. dupetithouarsii*: bright orange in *Pt. pulchellus* as against dark green and dark purple in *Pt. coronulatus*).

In short, in each pair, one member is emphasizing one set of elements in the general pattern, the other a different set, but the same two sets occur in both pairs.

Two interesting differences between the pairs can also be seen. In *Pt. mercieri* the malar apex is bright red, like the cap, and in *Pt. m. tristrami* but not *m. mercieri* the yellow hind border is very broad, bright, and well-marked. Neither of these characters are found in the New Guinea pair. A red, purple or blue malar spot is found in several isolated forms of the purpuratus subgroup. It is probably a stage in the blurring of the limits of the cap; this view is discussed below (p. 1402). The special interest of the malar spot in *Pt. mercieri* is that here alone it is large, conspicuous against the grey of the cheeks, and even provided with a narrow olive yellow hind-border, at least in *Pt. m. tristrami.* It is difficult to resist the conclusion that when the first invasion of the Marquesas occurred, the populations began to develop those trends characteristic of very isolated forms which are described below p. 1401. The abdominal spot or band was lost, the red of the cap began to spread to the face; but on the arrival of the second invasion, this process was checked, and the malar spot was actually turned to use as a specific recognition mark, being enhanced by increase in size, contrast with the clear dark grey of the cheeks, and by a bordering of olive. Similarly in *Pt. mercieri,* although the abdominal band or spot is lost, there is a clear contrast between the grey breast and yellow abdomen, their contiguous edges forming a definite transverse boundary.

Variation in the cap-border is found in both the Marquesan species. In the north, (*Pt. m. mercieri, Pt. dupetithouarsii viridior*) it is reduced in both species, being absent in *Pt. mercieri,* narrower, paler and less well-defined in *Pt. dupetithouarsii.* In the south *Pt. m. tristrami* has an exceptionally broad and bright yellow cap-border, which however is nearly equalled in breadth (not at all in brightness) by that of *Pt. purpuratus chrysogaster.* In *Pt. d. dupetithouarsii,* the border although narrow is conspicuous because there are considerable tinges of orange and even red in it. These variations are found together with a general tendency for diffusion of a yellowish tinge over the plumage in the north with consequent reduction of the purity of grey areas, a decrease in contrast between the breast and abdomen, and a reduction to olive of the cap-border in *Pt. dupetithouarsii.* Murphy (1924a) states that there seems to be a gradual change in the characters of *Pt. dupetithouarsii* from north to south. If so, the separation of this species into two subspecies is an over-simplification, and one should recognise a cline. Without extensive investigations in the wild, it is hardly possible to say more than that the clinal trend is seen also in *Pt. mercieri* and the factors most likely to affect both species are climatic.

The variation in the Marquesas pair is not parallelled exactly in the western pair, nor indeed would complete agreement be expected. In the western pair the yellow cap-border is very obvious in *Pt. coronulatus,* which has the less intensely coloured cap, and is the more obvious since the edge of the cap bordered by it is a much more intense purple than the rest. In *Pt. pulchellus* the rich red cap is not bordered, but as it is clearly marked off from the grey, greygreen and green of the lores and nape, possibly no extra accentuation is needed. This again is a question to be settled by experiment. Apart from such small differences, the similarity of organisation of the elements of the colour-pattern in *Pt. pulchellus* and *mercieri* on the one hand, and *Pt. coronulatus* and *dupetithouarsii* on the other, is most striking.

Both the western pair and *Pt. regina* overlap with *Pt. superbus,* in which the tendencies seen in *Pt. pulchellus* and *mercieri* are carried even further. The abdominal patch is white and separated from the dark grey breast by a large blue-black band, the cap is brilliant magenta, and the hind neck and upper mantle are a bright brownish red. There is also a humeral patch (blue-black in *Pt. superbus*), a feature found in several species groups but confined to the superbus subgroup in the purpuratus group. Again it is noteworthy that in the subspecies (*Pt. s. temmincki*) which occurs in the Celebes region, away from all other members of the purpuratus group, the breast-band, so conspicuous in *Pt. s. superbus,* is less well-marked. It grades into the breast anteriorly, so that only its posterior edge is clear-cut.

Pt. regina resembles *Pt. coronulatus* and *dupetithouarsii* in having a rather rounded patch of colour on the abdomen. The abdominal spot is present but not very clearly separated from the abdominal patch, nor contrasted as sharply with the breast as in *Pt. superbus* and *pulchellus,* or even *coronulatus.* There is no extension of deep green over the whole breast and sides, such as is a peculiar feature of *Pt. coronulatus* and *monacha,* and the breast, neck and head are much as in *Pt. superbus* except that the mantle is not brownish red, and the cap, which is less purple, has a clear yellow border. The red mantle, large abdominal bar, white abdominal patch and sexual dimorphism of *Pt. superbus,* which distinguish it clearly from *Pt. coronulatus* and *pulchellus,* separate it also from their geographical representative, *Pt. regina,* which forms with it a pair similar to those just discussed but with a greater degree of ornamentation.

It appears, then, that where closely related members of the purpuratus group overlap, one does find the preservation of distinctive features, even although one pair (*Pt. pulchellus* and *coronulatus*) are small forest birds in which the need for protection, that is for the extensive development of green areas, is felt, and another (the Marquesan species) is at the extreme edge of the range, in a very small avifauna and adjacent to forms (*Pt. purpuratus*) which have lost most of the complexity of their patterns. Indeed the maintenance (and apparent enhancement after overlapping) of distinctive patterns in the Marquesan species is almost as good a demonstration of the importance of specific recognition marks as is given by the species of *Sitta* described by Vaurie.

(ii) *Forms isolated on large islands or archipelagos.*

These forms may be expected to lose their distinctive patterns and to do so rather quickly, since they will be represented by large populations. Ripley and Birckhead (1942, p. 1395) mention that individuals of *Pt. porphyraceus* are often seen far out at sea. Occasional flights from one island to another may be expected, especially in archipelagos of very small islands (such as the Tuamotus) on each of which there is only a very limited supply of food, so that large archipelagos might be expected to function as single large island. In fact, there is a steady decline in the complexity of the pattern as one passes along the series *Pt. regina, greyii, porphyraceus, rarotongensis, purpuratus.* (*Pt. rarotongensis*, which is confined to one small island, is discussed below). *Pt. regina* overlaps with the rather closely related *Pt. superbus* and may be expected to keep some complexity. *Pt. porphyraceus* overlaps only with the highly modified *Pt. perousii* and the luteovirens species group. These are too different to be regarded as very close relatives.

(iii) *Forms isolated on small islands relatively near to large ones, or archipelagos.*

Such forms are likely to show evolutionary changes most quickly. As they inhabit very restricted and comparatively uniform localities, they are subject to selection pressures rather constant in direction, not to selection for a character in one part of the range and perhaps even against it in another part. Although their population-sizes are small, the chances of recruiting their genetic variability by occasional immigrations are high, while at the same time they are not so close to large islands or archipelagos as to be completely swamped by gene-flow and therefore unable to diverge from their parent stock. Consequently, with a high degree of genetical variability, and strong and constant selection, they will diverge rapidly. Examples here are *Pt. richardsii,* derived from *Pt. greyii* (which has also recently reinvaded the Solomons (Gower Island) from the south), and *Pt. regina xanthogaster* in the Banda Isles, Kei Isles, and easternmost Lesser Sunda Isles, which shows the same tendencies as *Pt. richardsii,* to extreme paleness of the head and neck, and reduction of bright reds and purples (except that its scapular spots have not become pink). Both forms are on islands which almost certainly have a comparatively reduced rainfall, and the general pallor is probably correlated with this.

(iv) *Forms isolated on small and remote islands.*

As Wright (e.g. 1948) and Fisher (1930) have both pointed out, when population size is very small there is much inbreeding with a consequent decrease in genetical variability, which is replenished by mutation only slowly. Consequently forms which are isolated on very small islands but not refreshed genetically by occasional immigrants may be expected to evolve only very slowly. Three forms appear to belong to this category, namely *Pt. roseicapilla, Pt. huttoni,* and *Pt. insularis.* Although *Pt. rarotongensis* might well seem to be another example, its almost perfect intermediacy in colour pattern between *Pt. porphyraceus* and *Pt. purpuratus chrysogaster,* suggests strongly that it does receive immigrants from both.

(a) *Pt. roseicapilla*

The remarkable resemblance of *Pt. roseicapilla* to the eastern Australian subspecies of *Pt. regina,* 1500 miles away and separated from it by *Pt. coronulatus, pulchellus, monacha* and subspecies of *Pt. porphyraceus,* has been pointed out by Ripley and Birckhead (1942, p. 1395). *Pt. roseicapilla* differs from *Pt. r. regina* in having a darker cap and abdominal spot, a less clear border of the cap, the hind neck rather greyer, and the tail band broader and less yellow, more greyish. In addition, the feathers of the malar apex are the same colour as the cap. (Ripley and Birckhead also describe as 'malar apex concolorous with the crown' such forms as *Pt. richardsii,* in which the crown has become pale and so resembles the neck and face generally. While both conditions may be covered by the same form of words, it is obvious that they cannot be called the same character). *Pt. roseicapilla* is as large as *Pt. r. regina,* and larger than the subspecies of *Pt. regina* in the Banda Sea region.

Of these characters, the resemblance in size between *Pt. roseicapilla* and *Pt. r. regina* is almost certainly a simple case of Bergmann's rule, these two being related forms with ranges confined to or partly in rather cooler regions than those inhabited by *Pt. r. ewingi, flavicollis,* or *xanthogaster.* There appears to be a cline of increasing size to the southward in *Pt. greyii* also (Ripley and Birckhead, 1942 p. 1395), and the two most isolated southern forms east of Fiji, *Pt. huttoni* and *Pt. insularis* are noticeably large (indeed, *Pt. huttoni* is the giant of the group).

There is also a tendency for forms wholly or partly in cooler regions (e.g. *Pt. huttoni, Pt. greyii, Pt. r. regina, Pt. porphyraceus hernsheimi* (Kusaie), *ponapensis* (Uala, Ponape) and *pelewensis* (Palau Is.) to have darker and more intense shades of red and yellow, as in *Pt. roseicapilla.* A red, purple, or blue malar apex occurs in other isolated forms, namely *Pt. monacha, huttoni* and *mercieri.* The slight obscurity of the yellow hind-border of the cap is seen in several forms, from *Pt. porphyraceus* eastwards. In some, e.g. *Pt. huttoni,* it disappears altogether, in others, e.g. *Pt. purpuratus chrysogaster* it widens but also darkens, becoming an ill defined olive area. Cott (1940) has shown that the apposition of bright and dark areas, well-defined where they are contiguous, is a device for enhancing the conspicuousness of either or both sorts of area—in this case, almost certainly for accentuating the cap. The obscurity of the border in isolated forms is therefore part of the general simplification and degradation of the pattern. A general greying of the hind neck (i.e. loss of yellow pigment) has the same sort of geographical distribution and significance.

It is probable that the spread of red or purple to the malar apex is also to be regarded as a degradation in that it tends to obscure the clear and distinctive shape of the cap. In *Pt. roseicapilla* the apical spot is small and not very clearly defined, while in *Pt. huttoni* its boundaries are made still less sharp by the presence of a wash of red over the chin also. It is quite large in *Pt. monacha* but again does not contrast with the green of the cheeks as the deep red cap contrasts with the dull grey of the malar apex and cheeks in *Pt. r. regina,* for example. But in *Pt. mercieri* it is a conspicuous object, for the reasons discussed above (p. 1398). The general spread of red on the face in *Pt. huttoni* is reminiscent of the general redness seen in *Pt. jambu,* which is also a very isolated form, overlapping only with the very different *Pt. porphyrea* in Sumatra.

It appears, then, that the special characters of *Pt. roseicapilla* are those of isolated forms. Its resemblance to *Pt. r. regina* is due partly to their being of the same stock, partly to a certain similarity of climatic conditions, and partly to the fact that *Pt. regina* overlaps with *Pt. superbus* and therefore still retains a rather complex pattern while *Pt. roseicapilla* has not yet been able to simplify its pattern very extensively.

(b) *Pt. huttoni*

This remarkable species bears much the same relationships to *Pt. porphyraceus, rarotongensis,* and *purpuratus* as does *Pt. roseicapilla* to *Pt. r. regina, greyii,* and *porphyraceus* respectively—that is, it is an isolated form preserving certain characters (large abdominal spot, rather dark emerald green or blue-green wing-covert spots) which tend to be lost in them, but diverging from them in a manner appropriate to very isolated forms. Its characters of size, colour, and malar apex have already been mentioned. In addition, it has the peculiarity that the under tail coverts are rather purplish red and the outer edges of the tertials, normally yellow, are pinkish. However, the under tail coverts of *Pt. greyii* are intermediate in shade between those of *Pt. huttoni* and *Pt. regina,* and it is interesting to note that the isolated member of the superbus superspecies, namely *Pt. perousii,* also has red under tail coverts (although yellow in the female of *Pt. p. mariae*). The pinkish edges of the tertials are unique. The lax and hairy plumage is also seen in *Pt. purpuratus* and *insularis.*

(c) *Pt. insularis*

This form is ranked as a subspecies of *Pt. purpuratus* by Ripley and Birckhead, but although there is much to be said for such an arrangement, its affinities are so complex that it is better to keep it as a distinct species. The subspecies of *Pt. purpuratus* are, from west to east:

Pt. p. chrysogaster	Western Society Isles (Borabora, Tahaa, Raiatea, Huaheine)
Pt. p. frater	Moorea
Pt. p. purpuratus	Tahiti
Pt. p. chalcurus	Makatea
Pt. p. coralensis	Tuamotu archipelago except Makatea

The first three form a cline of increasing simplicity of colour-pattern from west to east. *Pt. p. chrysogaster* is very similar to *Pt. rarotongensis* but has no trace of a red abdominal spot. Also the hindneck is greyer, the cap is pale lilac, not dark red, and the olive yellow border is wide and indistinct not narrow and well-marked. Both have an extensive yellow wash over the lower under parts. *Pt. p. frater* is rather smaller, with an even more indistinct cap and smudgy border. The under parts are more grey, less yellow, and the first primary is less clearly emarginate. Ripley and Birckhead consider that the plumage is even more fluffy and degenerate; this may be so, but the difference is not marked. *Pt. p. purpuratus* carries all these trends a stage further, since it has a duller lilac cap, particularly obscure anteriorly, a less well-defined border, still more general grey beneath and an even less emarginate first primary. Also, the tail-bar is grey, smaller, and clearly subterminal. The under parts are so generally grey that it is impossible to distinguish any trace of an abdominal and pectoral patch; the grey merely becomes gradually somewhat yellowish towards the lower abdomen.

Very remarkably, the cline is now reversed in some respects. *Pt. p. chalcurus,* has a cap as deep red as that of *Pt. rarotongensis,* with only traces of a dull yellow border, since the neck, breast and abdomen generally have a distinct wash of yellow, nearly as strong as in *Pt. p. chrysogaster,* and the border is therefore hardly distinguishable. Ripley and Brickhead saw two specimens with a faint orange wash on the abdomen. *Pt. p. coralensis* is to *Pt. p. chalcurus* very much what *Pt. p. purpuratus* is to *Pt. p. frater,* since it has a slightly paler cap incomplete in front (a character which appears also in *Pt. porphyraceus pelewensis*), and is greyer, with less of a yellow wash on the foreparts; because of this, the dull remnants of the hind border are actually more easily seen in *coralensis* than in *chalcurus.* The abdomen, however, is yellowish in both, and Ripley and Brickhead record that on some islands there is tendency for an orange wash to be present. Thus in these two forms, the usual colour-difference between the breast and abdomen reappears.

The distinctiveness of *Pt. p. chalcurus* is unexpected. As Murphy (1924b) pertinently remarks, "It is interesting that the uplifted and well-wooded coral island of Makatea, so different in superficial features from its neighbours among the Tuamotus, should not only share with Tahiti the large fruit pigeon, *Globicera aurorae,* but should also have an endemic *Ptilopus* markedly different from the widely distributed *P. coralensis."* Equally remarkable are the characteristics of *Pt. insularis,* confined to the remote Henderson Island. It is a rather large form with an intense red cap and very narrow, rather dull, border. The breast is a darker grey, so that the white chin-patch is much better defined, the abdomen is dull green and the back and bases of the bifid breast-feathers are also greener, while the emerald green areas on the wing coverts are darker. In fact, the red of the cap, the grey of the breast, and the clear separation between breast and abdomen are almost identically the same as is seen in *Pt. mercieri,* and the colours of the back and the wing covert spots are not dissimilar. Where *Pt. insularis* differs from *Pt. mercieri* it tends to resemble *Pt. p. coralensis* and *chalcurus,* but does not show much affinity with *Pt. dupetithouarsii,* the orange abdominal patch of which seems to link it directly to *Pt. p. coralensis.*

These facts, at first sight inexplicable, are partly comprehensible when the effects of divergent selection are kept in mind. The nature of the differences between *Pt. mercieri* and *dupetithouarsii* have been discussed already. It is certain that these forms arose from the same stock. Since both lack any definite abdominal spot or bar, it is reasonable to suggest that they arose from a form which had also lost it or was in the process of losing it. Selection in the area occupied by *Pt. purpuratus* acts to simplify the colour pattern and to produce a general paling (as in the Banda Sea region, and apparently also in the southern-most Solomons). The first invasion of this area was by a form not unlike *Pt. r. regina,* which also reached the Marquesas, and which proceeded to simplify and lighten its colour pattern. Before this process had gone very far, it reinvaded the Marquesas successfully, producing the paler form *Pt. dupetithouarsii.* The process of simplification which was going on also in *Pt. mercieri* was now stopped, and the differences between the two forms were intensified and sharpened. It seems that only on the more uplifted islands were the two species able to coexist. Subsequently, the populations in the Society Isles and Tuamotus continued to simplify, and are now *Pt. purpuratus.* It is obvious that the remarkable resemblances between *Pt. insularis* and *Pt. mercieri* are immediately explicable if *Pt. insularis* is to *Pt. mercieri* what *Pt. roseicapilla* is to *Pt. regina,* and *Pt. huttoni* to *Pt. porphyraceus, rarotongensis,* and *purpuratus,* namely a highly isolated form evolving only slowly and therefore retaining many characters modified in its close relatives, with the important difference that *Pt. mercieri,* because of its overlap with *Pt. dupetithouarsii,* has lost fewer characters than e.g., *Pt. rarotongensis* and *purpuratus,* and has actually intensified a few. The occasional orange wash seen in *Pt. p. coralensis* can reasonably be referred to slight gene-flow from *Pt. dupetithouarsii,* and the yellow abdomen of *Pt. p. chrysogaster* at the other extreme of the range to rare gene-flow from *Pt. porphyraceus,* an interpretation which is greatly strengthened by the very intermediate character of *Pt. rarotongensis.*

Of all these islands, Tahiti is by far the largest, and it is perhaps not surprising that the populations on it and the nearby island of Moorea should have gone furthest towards simplification, and loss of the specialization of the first primary which is found in all other members of the species-group. The distinctiveness of the population on Makatea remains unexplained, but almost certainly no *complete* explanation of the variation in *Pt. purpuratus* can be obtained until much more information is available about the exact habits and habitats of the different populations, the degree to which they are normally or occasionally nomadic, and the general characteristics of subspecies on small mountainous islands, as compared with those on atolls, in a number of unrelated species.

DISTRIBUTIONAL HISTORY

Ripley and Birckhead (1942) divide those forms that are distributed to the east of Australia and New Guinea into two subgroups. Subgroup B consists of *Pt. richardsii, greyii,* and *porphyraceus,* subgroup A of *Pt. rarotongensis, purpuratus* (including *insularis* as a subspecies), *huttoni, dupetithouarsii, mercieri,* and (less closely related) *perousii.*

They consider that the 'old stock' has given rise to one northward expansion producing *Pt. roseicapilla* in the Marianas, and two eastward ones, the first producing subgroup A, from Fiji eastwards to the Tuamotu archipelago, and the second subgroup B in Melanesia (*Pt. richardsii, greyii*) with a subsequent expansion to Fiji (*Pt. porphyraceus* and then northward to the Caroline and Palau Islands (*Pt. p. hernsheimi, ponapensis,* and *pelewensis*). The two Marquesan species are regarded as probably derived from subgroup B, and perhaps forming a subgroup by themselves. They are clearly the result of a double invasion of the Marquesas by the same stock (Mayr, 1940). On Ripley and Birckhead's hypothesis it is necessary to assume that the first eastward invasion was from New Guinea direct to Fiji or islands even further east, while the second produced the forms in the New Hebrides and southern Solomons which then were able to cross the enormous range occupied by the first invasion and invade the Marquesas twice.

This improbable hypothesis is based partly on a too rigid classification of the various forms into subgroups, and partly on a lack of consideration of the different effects likely to be produced by selection under different conditions. The characters given for the subgroups are inconstant and unsatisfactory, and *Pt. rarotongensis* (which was unfortunately not available to the authors) is a perfect transitional form, with remnants of a dark abdominal spot as in the 'old stock' and 'subgroup B' but also with emerald green spots on the scapulars and wing-coverts as in *Pt. purpuratus* and *huttoni*. In addition, *Pt. perousii* is almost certainly derived not from these forms but from *Pt. superbus* (Cain, 1953) and forms with it a separate superspecies. Ripley and Birckhead do not discuss the characters of the 'old stock,' the distributional history of which has been outlined above (p. 1395–1396).

When the effects of differential selection, as discussed above, are borne in mind, it is obvious that there is no reason whatever for postulating more than a single main expansion eastwards from the Australasian region, an expansion which flowed twice into the Marquesas, producing there first *Pt. mercieri* (with *Pt. insularis* as a relict form on Henderson Island), and later *Pt. dupetithouarsii*. These two, being in contact, have preserved, and even intensified, some complexities of the original colour-pattern, which in the Tuamotus and Society Islands has been rapidly and almost completely abandoned. On the more isolated islands evolutionary change has been slower. Also, it is almost certain that the climate of the more elevated islands is different from that of low-lying atolls, being probably cooler and wetter. If so, the comparatively large size and sombreness of plumage of *Pt. huttoni, insularis, roseicapilla,* and *purpuratus chalcurus* (Makatea) are in part a response to local conditions, contrasting with the paleness seen in *Pt. regina xanthogaster, Pt. richardsii,* and *Pt. purpuratus coralensis.* The populations of *Pt. purpuratus* in the Society Isles form an apparent exception which requires investigation. The possibility of slight gene-flow in maintaining certain characteristics has already been mentioned (p. 1400, 1405).

It would seem, then, that the purpuratus species-group originated in the New Guinea region, and gave rise to two main branches. One is now represented by *Pt. superbus,* still centred there, and *Pt. perousii* in Fiji, which has many of the characteristics of an isolated form (Cain 1953). *Pt. superbus* has an enormous range, with only one subspecies. Either it has expanded very recently or there is continual gene-flow between islands, which has prevented subspeciation except in the isolated Celebes region; field investigation may allow a choice of one of these alternatives to be made.

The second branch speciated within New Guinea, giving rise to *Pt. coronulatus* and *pulchellus,* and also expanded enormously to the north (*Pt. roseicapilla*) and to the south (*Pt. regina*) and then eastwards to the Marquesas and Henderson Islands. Several subsidiary expansions can be recognized, e.g. *Pt. regina* to Timor and the eastern Lesser Sunda Isles, *Pt. greyii* to the Solomons, *Pt. porphyraceus* to the Carolines and Palaus, and most important, the proto-*purpuratus* a second time into the Marquesas, producing *Pt. dupetithouarsii.* This proposed distributional history of the purpuratus species-group, it is believed, fits the known facts of geographical variation in the group, and gives sufficient weight to the effects of divergent selection.

CLASSIFICATION

While it is obvious that here, as elsewhere, no simple system of taxonomic ranks can express the full complexity of the relations between species, nevertheless a more natural arrangement of the purpuratus group than those proposed so far can be produced. The arrangements of Salvadori (1893) and Peters (1937) were made solely on the basis of plumage and other characters with no reference to the geographical facts, and little realization of the possibilities of convergence and divergence. To place *Pt. mercieri* next to *Pt. r. regina* and then follow the pallid subspecies of this species with the pallid *Pt. dupetithouarsii,* is unsatisfactory; and in this and other respects the arrangement proposed by Ripley and Birckhead is a considerable improvement. But it is clear that among the 'old stock' treated by them as a sample group of geographical representatives, there have been great changes, and that *Pt. pulchellus* has as good a claim as *Pt. coronulatus* to be placed in the same superspecies as *Pt. regina*. Similarly both *Pt. mercieri* and *dupetithouarsii* are representatives of *Pt. purpuratus,* and *Pt. insularis* links *Pt. purpuratus* with *Pt. mercieri.* Also, the removal of *Pt. perousii* from the purpuratus subgroup to the superbus subgroup not only brings its peculiarities into line with those of other insular forms (Cain 1953) but renders unnecessary the complex hypothesis of invasions proposed by Ripley and Birckhead. The situation is more like that proposed (in a map) by Mayr (1940).

There is no doubt that *Pt. roseicapilla, regina, richardsii, greyii, porphyraceus, rarotongensis, purpuratus* and *huttoni* form a single superspecies, as Ripley and Birckhead have shown. (Indeed, it would not be unreasonable to combine *Pt. porphyraceus, rarotongensis* and *purpuratus* into a single species). *Pt. insularis* is also a geographical representative of these, and must be included. It is probable, as shown above, that *Pt. dupetithouarsii* is the later arrival in the Marquesas and the more directly related to *Pt. purpuratus,* so that it too could be added. But almost as good a case could be made out for adding instead *Pt. mercieri* which is connected with *Pt. purpuratus* via *Pt. insularis.* In New Guinea the situation is worse, because there is no reason to believe that *Pt. pulchellus* and *coronulatus* were not produced simultaneously and side-by-side on two separate islands in this area which have since joined together and there is no reason to choose one form rather than the other. Further, *Pt. monacha* is obviously more closely related to *Pt. coronulatus* than to any other species, although it is a geographical representative of *Pt. regina* and its allies. The situation is best expressed diagrammatically:—

monacha — *coronulatus* ⟍
⟩ *regina, roseicapilla, richardsii, greyii* etc.
pulchellus ⟋
mercieri
. . . *purpuratus* *insularis*
⟍ *dupetithouarsii*

Accordingly, in the classification given above (p. 1394) I have referred to the whole purpuratus subgroup as a single superspecies with two *doublets*. If a triple invasion had occurred, the three species concerned would have been bracketed together as a *triplet*, and so on. This simple convention indicates clearly the relationships of the species concerned, while obviating the necessity of choosing one of a pair of equally divergent sympatric forms to be admitted to a superspecies. It is obviously necessary to use brackets only to indicate the coexistance of forms immediately descended from a common ancestor. To use them for other overlaps, e.g. that of *Pt. monacha* and *Pt. hyogastra,* would be absurd.

SUMMARY

1. In the *Ptilinopus purpuratus* species-group, forms living under different ecological conditions have diverged greatly in plumage and other characters.
2. When closely related forms overlap, they maintain complex colour patterns, one form emphasizing certain elements of the general pattern, the other exaggerating different ones. This is found especially in two New Guinea and two Marquesas species.
3. Forms isolated without contact with close relatives tend to lose their complex patterns. The rate of loss depends on the degree of geographical isolation.
4. Recognition of the divergent effects of selection under different ecological conditions allows a more satisfactory distributional history to be constructed, and a more natural classification than can be induced from the mere examination of plumage characters without reference to the facts of geographical distribution.
5. The use of brackets for indicating multiple invasions by closely related species is exemplified.

REFERENCES

CAIN, A. J. 1953. Affinities of the fruit pigeon *Ptilinopus perousii* Peale. *Ibid.*, in press.

CAREY, S. W. 1938. The morphology of New Guinea. *Australian Geographer, 3*: 3-30.

COTT, H. B. 1940. *Adaptive coloration in animals.* xxxii + 508 pp., 1 pl., 84 text-figs. London.

FISHER, R. A. 1930. *The genetical theory of natural selection.* xiv + 272 pp., 2 pl., 11 text-figs. Oxford.

LACK, D. 1947. *Darwin's Finches.* x + 208 pp., 8 pls., 27 text-figs. Cambridge.

MAYR, E. 1940. Speciation phenomena in birds. *Amer. Nat.*, 74: 249-278.

————. 1941. *List of New Guinea Birds.* xi + 260 pp., 1 map. New York.

MURPHY, R. C. 1924a. Birds collected during the Whitney South Sea Expedition. 1. *Amer. Mus. Novit., 115.*

————. 1924b. Birds collected during the Whitney South Sea Expedition. 2. *Amer. Mus. Novit., 124.*

PETERS, J. L. 1937. *Checklist of Birds of the World, 3.* xiii + 311 pp. Cambridge (Mass.).

RIPLEY, S. D. and BIRCKHEAD, H. 1942. Birds collected during the Whitney South Sea Expedition. 51. On the fruit pigeons of the *Ptilinopus purpuratus* group. *Amer. Mus. Novit., 1192.*

SALVADORI, T. 1893. *Catalogue of the Columbae, or Pigeons* . . . xix + 676 pp., 15 pls. London.

TINBERGEN, N. 1948. Social releasers and the experimental method required for their study. *Wilson Bull.*, 60: 6-51.

————. 1951. *The study of instinct.* xii + 228 pp., 1 pl., 130 text-figs. Oxford.

VAURIE, C. 1950. Notes on some Asiatic nuthatches and creepers. *Amer. Mus. Novit., 1472.*

————. 1951. Adaptive differences between two sympatric species of nuthatches (Sitta). *Proc. 10th int. orn. Congr. Uppsala June 1950,* 162-166.

WRIGHT, S. 1948. On the roles of directed and random changes in gene frequency in the genetics of populations. *Evolution, 2*: 279-294.

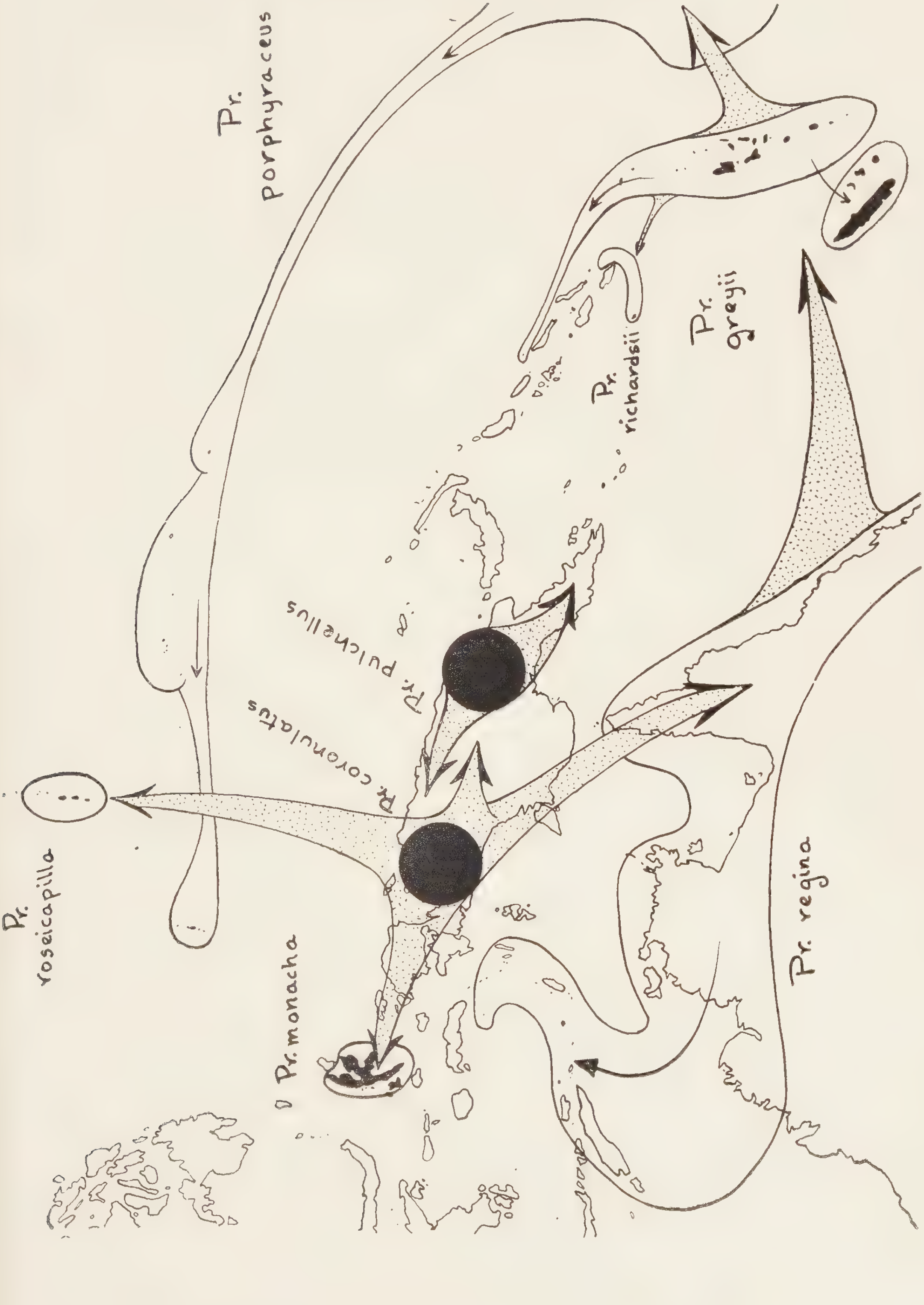

Pr. porphyraceus
Pr. roseicapilla
Pr. monacha
Pr. coronulatus
Pr. pulchellus
Pr. richardsii
Pr. greyii
Pr. regina

FIGURE 1

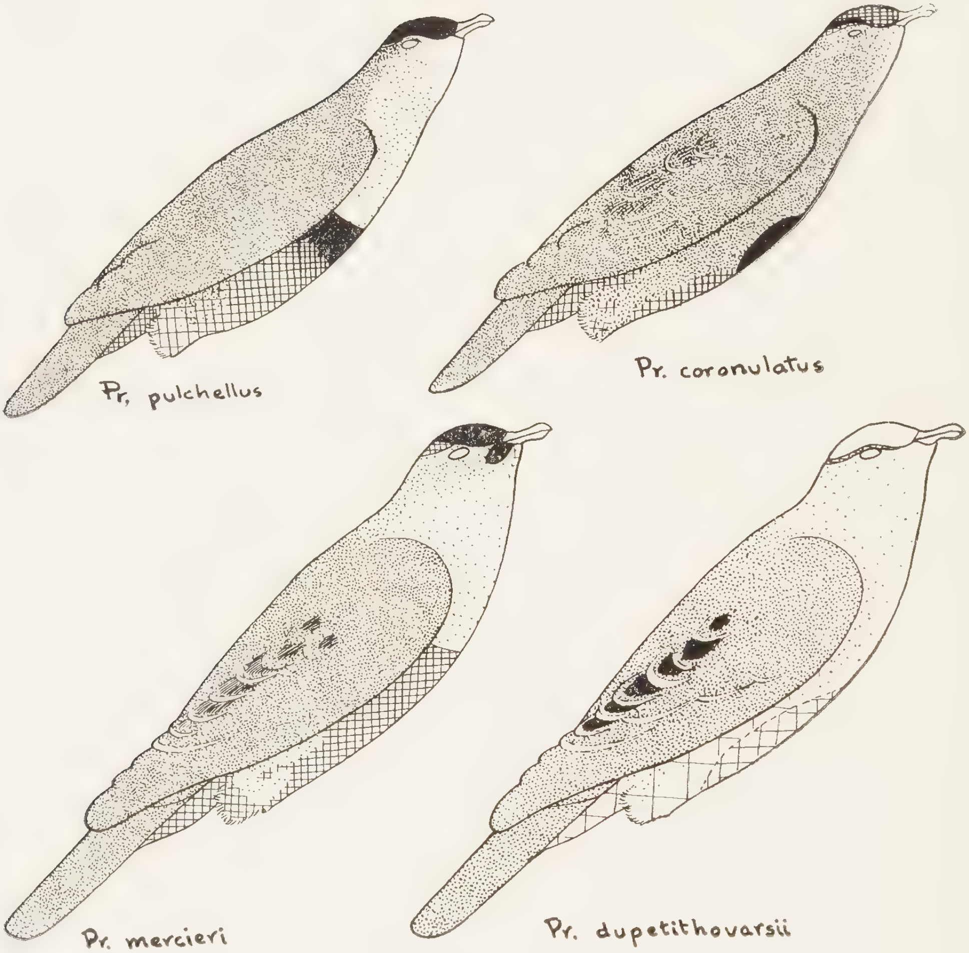

Pr. pulchellus
Pr. coronulatus
Pr. mercieri
Pr. dupetithouarsii

FIGURE 2

ENTOMOLOGICAL AND PLANT PEST AND DISEASE CONTROL WORK IN THE PHILIPPINES WITH SPECIAL REFERENCE TO THAT OF THE BUREAU OF PLANT INDUSTRY ON THE MIGRATORY LOCUST AND OTHER MAJOR PESTS AND DISEASES OF CROPS

By Faustino Q. Otanes[1]
Bureau of Plant Industry
Department of Agriculture and Natural Resources
Manila, Philippines

In two papers read in the past two Pacific Science Congresses, that of California in 1939 and that of New Zealand in 1949, the writer gave accounts of entomological and plant pest control work in the Philippines. In the first paper, the work done especially in economic entomology during the Spanish and American regimes up to 1939 was reviewed. However, the most outstanding works in systematic entomology published by foreign or non-resident workers were enumerated. The second paper read in New Zealand discussed what had been done on entomological research from 1939 to 1949 by the Bureau of Plant Industry and the College of Agriculture, University of the Philippines, and in pest control by the former. In the latter paper, under entomological research, the writer summarized what has been published on breeding grounds and periodical outbreaks of the Oriental Migratory Locust by Uichanco (1936, 1937 and 1938), Otanes (1925, 1938 and 1940), and others.

The present paper treats of the work of the Bureau of Plant Industry since 1949, especially with reference to that on the Oriental Migratory Locust, *Locusta migratoria manilensis* Meyen, armyworms, particularly the grass armyworms, *Spodoptera mauritia,* rice stem borers (*Schoenobius incertellus* and *Scirpophaga innotata*) and rats, especially field rats, *Rattus rattus mindanensis,* and others.

The Oriental Migratory Locust
(*Locusta migratoria manilensis* Meyen)

As stated in the writer's paper presented in New Zealand in 1949, this insect is still one of the major pests of crops in the Philippines.

---

[1] Chief, Plant Pest and Disease Control Division.

Alarming outbreaks still occur at intervals, resulting in the destruction of more or less large areas of food crops, particularly rice and corn. However, invasions by huge devastating swarms are no longer general, as were otherwise the case during the Spanish regime and even during the early years of the American regime, when swarms migrating northward reached as far as Formosa (Taiwan). This was the reason why before World War II, Japanese entomologists took an interest in the study of locust outbreaks in the Philippines. Koidsumi and Ogasahara, for instance, published a paper (1940) entitled "The Philippine Locust and Its Relation to Taiwan (A climato-ecological consideration)" in the *Journal of Tropical Agriculture*, Japan, 12, No. 4 (December). That the Oriental Migratory Locust is not as destructive now as it used to be in the past has been due chiefly to the better organized campaigns against it and the more effective means of fighting it, especially now that more powerful new insecticides, like DDT, aldrin, dieldrin, and benzene hexachloride, have come into use.

As has been stated, outbreaks of the Oriental Migratory Locust occur at intervals, each outbreak cycle lasting a number of years. The duration of a cycle is certainly shortened or cut short by the campaigns waged. They lessen the densities of swarms and hasten the development of the insects to the phase *transiens* (subphase *dissocians*) and eventually to the solitary stage. Undoubtedly, natural enemies, especially birds, mites and parasitic insects play a helpful role to this end.

From the continuous records and charts of locust infestations of the Bureau of Plant Industry (formerly the Bureau of Agriculture) the following complete outbreak cycles have been definitely identified:—

1919 to 1929
1932 to 1939
1941 to 1949
1952 to the present (Only Burias Island is infested at this writing, November, 1953)

From our studies in the Bureau of Plant Industry, the following information, among other things, about these outbreak cycles has been obtained:—

1. There is an interval of one to three years during which only solitaries and loose or *transiens* swarms are found, the latter appearing later within the period. Thus after the 1919–1929 cycle, there were no migratory swarms in 1930 and the greater part of 1931. Again, after the 1932–1939 cycle, there were no migratory swarms in 1940 and the greater portion of 1941; and again after

the 1941–1949 cycle, there were no migratory swarms in 1950 and 1951.

2. The sporadic occurrences of loose or *transiens* swarms have proved so far to be a practical basis for predicting the probable beginning of an outbreak, that is the appearance of huge, dense and voracious migratory swarms.

The remaining small swarms of the 1941–1949 outbreak cycle were eventually exterminated by the middle of 1949 and the country was then declared free of locusts and remained so up to the end of 1951. However, loose or *transiens* swarms were reported in the Lagao area in the Southern Cotabato, Mindanao, early in 1952. Control work was therefore started by the Bureau of Plant Industry in cooperation with the Land Settlement Administration (LASEDECO) and the settlers. The small scattered swarms in the Lagao area estimated in the aggregate at not more than 2.5 hectares were soon controlled by spraying with Bladex F_2 (1 to 400 to 800 parts of water), and since that time more small swarms were found in several other places but an outbreak has not occurred up to this time in Cotabato, although that province has been considered as the chief permanent breeding place or outbreak area of the Migratory Locust. Small mixed swarms (consisting of solitaries and other locusts of the *transiens* phase) also occurred in nineteen (19) other provinces, namely, Palawan, Leyte, Sorsogon, Samar, Marinduque, Davao, Bohol, La Union, Ilocos Norte, Camarines Sur, Isabela, Cagayan, Zamboanga, Albay, Bukidnon, Abra, Misamis Oriental, Iloilo and Capiz.

The origin of each of the 1919–1929, 1932–1939 and 1941–1949 outbreak cycles has been traced to Cotabato province. That an outbreak in Cotabato has not occurred so far, may be partly due to the extermination of the incipient swarms, which would have multiplied to large swarms if they had not been promptly killed. The settlement and cultivation of large portions of Southern and Central Cotabato and other sections of that province may be another reason. It is known that the settlement and cultivation of the permanent breeding grounds or outbreak areas and outbreak centers tend to change ecological conditions in those areas, thus making difficult or impossible the development of the locusts from the solitary phase to the migratory phase. Examples in other countries of migratory locusts that have been permanently controlled by the settlement and cultivation of their breeding grounds can be cited.

By the middle of 1952, an alarming outbreak occurred in Masbate province. This was quite unusual, for Masbate has not been considered as a permanent breeding place or outbreak area of the Migratory

Locust. As early as February, 1952, scattered *transiens* swarms were reported from Burias, one of the islands comprising that province. Burias (Plate I, Fig. 1) has an area of about 42,000 hectares (162 square miles). It is a sparsely populated hilly island. There are no roads but only trails. Transportation from one place to another is chiefly by sailboat. Before the last World War the island was devoted chiefly to cattle raising. But during the War all the cattle were killed. Since then cattle raising on the island has not been rehabilitated and only small portions of the island are cultivated to crops, especially rice and corn. The undisturbed condition of the island has apparently been favorable to the development of locust swarms, aside from the probable influence of weather conditions. Before and in the early stages of the infestations prolonged dry spells were reported. Droughts have been associated with the occurrences of outbreaks. Locusts are known to be sensitive to high temperatures and low humidities, conditions which prevail during prolonged droughts and which stimulate the development of the insects from the solitaries to the *transiens* and migratory stages or phases.

Soon after infestations were reported from Burias in February, 1952, control work was started by the Bureau of Plant Industry. However, because of the scarcity of transportation facilities and because of adverse conditions prevailing on the island, such as presence of malaria and of dissidents, lack of water, etc., the control personnel of the Bureau of Plant Industry and their hired laborers could not cope with the situation. The greater portion of the island could not be covered, so breeding of the locusts was almost uninterrupted in most parts of Burias, and by June, 1952, large swarms of flyers had developed and migrated to the main island of Masbate and to Ticao, destroyed rice and corn fields and coconuts, and laid eggs in many parts of the province. Masbate proper, like Burias, was devoted chiefly to cattle raising. As in Burias, most of the cattle were killed and the land has been chiefly undisturbed, thus apparently making conditions favorable to locust breeding and multiplication. Small portions of the swarms that migrated from Burias to Ticao and Masbate proper were able to reach some islands of Leyte (especially Maripipi and Biliran) and also the northern part of Leyte proper, Samar (especially the Naranjo Islands, Tagapulan and Almagro), Sorsogon, Albay and Camarines Sur. Only a few stragglers reached Samar proper.

The usual ground methods of control were employed against the locusts, namely, application of poisoned bagasse bait, spraying with DDT-emulsion, soap solution, dusting with calcium arsenate and driving the hoppers into corrals and pits and beating them and catching the flyers with nets. After a series of laboratory and field tests, in which their effectiveness were verified, new powerful insecticides, especially aldrin and dieldrin, were used. However, even with the use of these and the acquisition of more ground equipment, such as hand pumps and power sprayers, the campaign was not forging much ahead because of transportation difficulties. The problem was to destroy as fast as possible the locusts in Masbate and in those few provinces, where portions of the Burias swarms have migrated and laid eggs, and thus prevent further spread and migration to other provinces, especially in Luzon, where campaigns in the uncultivated areas would be more difficult than in former years, chiefly because of the presence of dissidents. The only solution to the problem was the use of airplanes to exterminate the locusts rapidly. Negotiations were accordingly made by the Department of Agriculture and the Bureau of Plant Industry for the services of local planes.

AIRPLANES USED IN THE CAMPAIGN

As a result of the negotiations and representations made by the Department of Agriculture and the Bureau of Plant Industry, five (5) planes were used for the aerial spraying of locust swarms in the Province of Masbate. One of these was a hired plane, belonging to the Philippine Airways Corporation (PACO). It was a piper cab plane, a super cub (Plate I, Fig. 1-A), type commonly used in the United States for dusting and/or spraying against grasshoppers and of the type used in the middle East for spraying against swarms of the Desert Locust, *Schistocerca grogaria.* It had a spray tank with a capacity of 62 gallons and a long spray tube extending on each side to near the tip of the wing. The liquid was pumped out of the tank while the plane was in flight by a small propeller and the spray was dispersed by the plane's propeller in droplets and fine mists through twenty-four (24) nozzles, 12 on each side which are 10-½ inches apart.

The other planes used were a piper cub plane (L–5), formerly used as an ambulance plane, belonging to the Civil Aeronautics Administration (CAA), and two planes belonging to Philippine Airforce (PAF). These PAF planes were of the double winged type. (Plate I, Fig. 2-B). They were training planes (PT–13) of the Philippine Airforce and each was provided with a gravity type of spray equipment. The tank had a capacity of 45 gallons, with a spray tube of about 8 feet and 9 inches long with twenty-two circular holes or apertures two and a half inches apart, through which the spray passed out to be blown in mists by the violent air current generated by the force of the propeller. The CAA piper cub plane had at first a spray equipment similar to that of the hired plane, the PACO plane, but it was found defective and was changed to that of the gravity type. Its spray tube was about as long as that of the PAF plane. The tank had a capacity of 41 gallons. Another CAA plane, a small piper cub (L–4), was sent later to Masbate but this was not found suitable for spraying over the rugged terraine in Masbate and was most of the time grounded.

The CAA and PAF planes were detailed to the locust campaign in accordance with an authority given by the President of the Philippines in a Cabinet meeting. The Bureau of Plant Industry, however, paid the travelling expenses and per diems of the aviators and their mechanics.

Aerial Spraying with Aldrin, Dieldrin, etc.

The hired plane belonging to the Philippine Airways Corporation (PACO) arrived at Masbate late in the afternoon of September 2, 1952. It was piloted by Mr. W. P. Onstott, who has had previous experience with the use of planes for grasshopper control in the United States. The plane began spraying with aldrin in the morning of September 3, 1952. (Plate II, Fig. 1). At that time, young flyers that were developing from scattered bands of hoppers that hatched from eggs laid by swarms that migrated from Burias by the middle of June, 1952, were gathering into swarms. The spray used was 1 part of aldrin to 30 parts of water by volume. At the request of the pilot, the tank of the plane was given only a half load of spray (1 part aldrin to 30 parts water by volume). The plane took off from the airfield of Masbate, Masbate, at 7:45 a.m. on September 3, 1953, and sprayed a swarm on a ranch at Sitio Cadungondungon, which is about 16 kilometers southeast of the capital (Masbate). The plane landed back on the airfield at 8:10 a.m. Therefore it took the plane about 25 minutes to dislodge its spray load of 31 gallons and return. The plane took off again for Cadungondungon at 8:45 a.m., with a load of 52 gallons of spray (2 gallons of aldrin and 50 gallons of water) and landed back at 9:15 a.m., or 30 minutes later. The plane took another load, taking off at 11:05 a.m. and landed back on the airfield at 11:35 a.m. It sprayed both swarms in flight and those resting on grasses and shrubs and bushes.

Late in the afternoon when observations of the result of the spraying were made, many dead and dying flyers were found scattered on the ranch and in nearby areas, including the roads and ditches.

At about 5:00 p.m. in the afternoon that day (September 3, 1952), a large thick swarm of young flyers had settled for the night on a field by the provincial road at kilometer 11 at Malinta, a barrio of the provincial capital. The swarm occupied about 5 hectares of grassland and rice field. The land was somewhat rolling and there were a number of coconuts and other trees here and there along the borders of the area where the swarm had settled.

The plane started spraying at about 5:00 p.m. The spray load was 2 parts of aldrin and 50 parts of water by volume.[2] The plane swooped over the area a number of times, flying so low and avoiding the obstacles, especially the coconuts and other trees, that there was no doubt that the spray from the plane hit the objective. The spraying lasted about 20 minutes, the plane having dislodged all its load in that length of time.

Early in the morning of the following day, September 4, 1952, the result of the spraying was examined. The field was found literally covered with dead and dying locusts. Those dying and still able to jump showed tremors on their legs, which were indications of the effect of aldrin, a nerve poison. The nervous system being affected, the insects died of paralysis. Large numbers of the locusts, after having been affected by the aldrin spray, jumped from the field into a creek, where they died (Plate II, Fig. 2). It was estimated that practically the whole swarm was destroyed on the spot. The few flyers that were seen flying from the area probably consisted of those that were not hit by the spray and later joined other swarms.

Previously, there were doubts as to the practicability of using airplanes for spraying against locusts in Masbate, because of the rugged, hilly terraine, and because of obstacles, such as numerous trees. Operations under such conditions were considered risky. The result of the actual spraying at Malinta, however, dispelled all doubts as to the practicability of using airplanes over Masbate and similar other regions of the country for locust control, especially against thick resting or flying swarms. Safe flying over such areas really depended on the skill of the aviator and the suitability of the plane for low flying over such areas (Plate III, Fig. 1).

After this spectacular result at Malinta, efforts were made to keep all the planes detailed to the campaign in as active operations as possible, in order to cope with the serious situation, which greatly alarmed the people in Masbate and which received much publicity in the Manila press, so much so that Cabinet action with respect to the needs of the campaign became necessary. While it was thought more economical and more effective to have the planes spray swarms, preferably early in the morning and late in the afternoon when the swarms were on the grasses and shrubs and trees, yet when the planes were in good flying condition and the weather permitted, the aviators had to fly even towards noon and during early hours in the afternoon to locate and spray swarms reported by farmers, municipal officials and other parties, even when such swarms were in flight, to kill as many of the insects as possible and prevent them from destroying crops, as well as from flying to other provinces. It was especially urgent for the aviators to fly when the swarms were so large that when they alighted on rice and corn in particular they would cause much destruction or wipe out entire fields of rice and corn and defoliate large numbers of coconuts. It was observed that once the insects were wet with the spray their nervous system appeared affected and fed but little or not at all. The deadly effect of the aldrin spray was observed more clearly when swarms were sprayed by the planes late in the afternoon when they were settled on the grasses and other vegetation for the night. Most of the insects died on the spot (see Plate III, Fig. 2). When swarms were sprayed in the morning most of the insects still had a chance to fly and, dropping one by one, died in different places.

---

[2] Throughout the campaign, the average proportion of aldrin and water was 1 to 30 by volume, respectively. With dieldrin the proportion used was 1 to 40. These dilutions were found to be the most satisfactory, considering the immediate objectives of the campaign.

Summary of Aerial Spraying

The attached table shows the spraying accomplishments of the five planes from September 3 to December 31, 1952. The number of swarms of flyers destroyed was 518 which all in all amounted to about 5,998 hectares. These swarms ranged in size of from about two hectares to 200 hectares. A total of 417 hectares of hoppers were also destroyed.

As a result of the extensive and intensive airplane spraying in Masbate since September 2, 1952, that province was practically freed of adult locust swarms before the end of December, 1952. This has been made chiefly possible with the use of aldrin and dieldrin, which was also employed to a certain extent. From the spectacular result obtained in Masbate with these new powerful insecticides, it is believed that future infestations will be similarly cut short and the country will no longer be subject to general invasions, as were usually the case in the past, provided of course, that adequate means and facilities are made available sufficiently well in advance so that incipient swarms could be destroyed at once.

The suppression of the locust outbreak in Masbate with the use of airplanes and modern insecticides has been acclaimed as a classic in locust control in the Philippines. The infestations would have spread widely in Luzon and in the Visayas if they had not been wiped out promptly with such modern facilities.

Other Pests and Diseases

Besides the Oriental Migratory Locust, among the other pests and diseases to which the Bureau of Plant Industry has directed its attention in an effort to help farmers at least minimize their damages are rats, armyworms, rice borers, rice leaf hoppers, rice bugs, corn borers, abaca mosaic disease, coconut "kadang-kadang", coconut leaf miner, coconut black beetle, coconut slug caterpillars, citrus rind borer, citrus green bug, mango hoppers, onion thrips, etc.

Rats, armyworms and rice stem borers and other cereal pests, abaca mosaic disease and coconut kadang-kadang in particular, have received special attention and action, so much so that funds for their control have been provided under the FOA (MSA)–PHILCUSA assistance program.

Cereal Pests

Rats have been causing more or less serious destruction in many provinces. In some provinces, like Mindoro and Cotabato, rats have been alarmingly serious. In Western Mindanao, rats appeared to be an unmitigated evil for many years. Their recent depredations in Cotabato have attracted national attention. Contrary to press reports, however, their destruction to the rice crop in Cotabato has not been total. The greater portion of rice crops of that province has been saved. More or less serious damages have been done in certain sections, especially in the upper valley, because of the lack of baits which the farmers had to provide. In the lower valley of that province most of the rice crop has been saved, because farmers have been more alert and cooperative. The saving of the rice and corn crop has been due largely to the use of a modern poison, WARFARIN, supplemented by that of white arsenic and calcium cyanide or cyanogas. Where farmers have given their full cooperation to the Bureaus of Plant Industry and Agricultural Extension, the use of Warfarin in different provinces including Mindoro has given amazing results.

Outbreaks of armyworms, particularly the grass armyworm (*Spodoptera mauritia*), have occurred yearly since 1949 in varying proportions causing more or less serious damages to rice seedlings. Wettable DDT and DDT-oil emulsions have been used effectively against the worms.

During the last several years, rice stem borers, of which *Scheonobius incertellus* and *Scirpophaga innotata* are the most common, have attracted more attention because of their conspicuous damages, especially when the rice is heading.

In the search for more basic data on rice stem borers and other rice pests as well as diseases, two laboratories, one in Maligaya, Muñoz, Nueva Ecija, and another in Santa Barbara, Iloilo, have been built under the FOA–PHILCUSA program. An important phase of the research with reference to rice borers is the laboratory and field tests with modern insecticides, such as EPN–300, parathion, DDT, dieldrin, etc., as sprays to control the borers. In this work, as well as in the whole control program on cereal pests, we have the valuable cooperation and advice of Dr. Henry K. Townes, Entomologist of the FOA, who is consultant for the Bureau of Plant Industry.

The Abaca Mosaic Disease

Before the last war, the Bureau of Agriculture and the Bureau of Plant Industry succeeded in controlling the bunchy top and mosaic disease of abaca. In Davao, the mosaic disease was then considered a minor disease of abaca. But during the war, when abaca plantations were neglected, the disease had a chance to spread. After liberation, squatters took possession of the plantations, especially those formerly owned by the Japanese, and abused them by overstripping and planting corn in between the abaca plants. These practices fostered the spread of the disease until in many plantations, the infection varied from 50 to 100%. This alarmed the planters in Davao who clamored for help from the government.

In response to this clamor, the Bureau of Plant Industry launched a campaign against the disease in 1949. With more funds the Bureau's eradication personnel in Davao have been increased and many plantations have been freed of the disease. The eradication of the disease in abaca plantations has been made faster by the use of 2,4-D weedicides, which were found highly effective in killing the diseased plants to prevent the spread of the malady.

With funds made available under the FOA (MSA) assistance program, extensive and intensive eradication has been made possible and many plantations have been treated and re-treated and saved from being over-run by the disease. Dr. Otto Reinking, plant pathologist and former adviser under the Point Four Program, has given valuable advice and assistance, and more recently, Mr. Joe E. Walker, Agricultural Production Adviser of the FOA, has likewise given helpful advice and assistance to the program.

Research work on the disease has been given more impetus and as a result more basic information useful in the control has been obtained.

One important phase of the research program is the work on resistance with a view to isolating or developing certain varieties or strains of abaca resistant to the disease.

Coconut "Kadang-Kadang"

At present, the most important disease of coconuts being tackled by the pathologists and entomologists of the Bureau of Plant Industry is the so called "kadang-kadang" disease of coconut. This is very serious, particularly in the Bicol provinces, millions of trees having been affected. The definite cause of the malady is not yet known, although from indications, it is believed to be due to a virus, but this has not been definitely proven. Extensive and intensive work on transmission is being done to ascertain whether the disease is due to a virus.

Many species of insects, particularly sucking insects, such as mealy bugs, scale insects, aphids and leafhoppers, of which there are quite a number, have been found abundant on coconut in the Bicol region, and there appears to be no doubt that they play an important role in devitalizing coconuts, which sooner or later show typical "kadang-kadang" symptoms: yellowing, mottling, shortening of the leaves, sterility, tapering of the trunk and eventually, death. These sucking insects are tended by ants which help foster their spread and multiplication. Experiments are in progress in the Guinobatan Abaca Experiment Station of the Bureau of Plant Industry with a view to finding the most effective insecticides against them and the ants that foster their spread and increase.

Dr. Donald de Leon, former entomologist with the FOA (MSA), served as consultant for this FOA–PHILCUSA–supported kadang-kadang research project.

OTHER ENTOMOLOGICAL AND PLANT PATHOLOGICAL RESEARCH PROJECTS

Besides the research projects indicated in connection with cereal pests, abaca mosaic and kadang-kadang, the following other research projects are in progress. These indicate our most important plant pest and disease problems and the phases of these problems that are being tackled by technical men of the Bureau of Plant Industry as a part of the whole program for the improvement of the various crops:

Rice Pests and Diseases

1. Studies on the relative susceptibilities of different varieties of rice to stem borers with a view to encouraging the general planting of the varieties found least susceptible, if such varieties possess other desirable qualities.
2. Further studies on the rice stunt disease, rice blast and other important rice diseases.
3. Studies on the relative resistance of different varieties of rice to rice blast, leaf spots and other diseases.
4. Field tests on different planting dates with the object of avoiding injury by rice stem borers.

Corn Diseases

1. Field tests with different varieties and strains of corn to determine their resistance to corn rust.

2. Studies on the relative resistance of different varieties and strains of corn to the yellow stripe disease of corn.

3. Hybridization and selection with certain varieties of corn to develop strains resistant to the yellow stripe disease.

4. Introduction of insect parasites and disease organisms for the control of corn borer and other corn insects.

5. Tests with different chemicals to control the corn weevil and other stroed grain pests.

Abaca Mosaic Disease

The following are the other research projects in progress at the Abaca Experiment Station at Bago-Oshiro, Davao:

1. Transmission studies on banana mosaic.

2. Studies on abaca mosaic spread with the object of formulating more effective control measures.

3. Further studies on insect and other vectors of abaca mosaic.

4. Studies on systemic insecticides with a view to controlling the vectors and the mosaic disease.

5. Further studies on the food plants of the abaca mosaic vectors, *Aphis gossypii, Aphis maidis, Proutista moesta,* etc.

Coconut Kadang-Kadang

Following are the research projects on kadang-kadang at the Experiment Station at Guinobatan, Albay:

1. Epidemiology studies on coconut kadang-kadang with a view to ascertaining rate and means of spread.

2. Transmission of coconut kadang-kadang with the use of dodder, *Cassytha* sp. The method consists in establishing the parasite on a diseased plant and later attaching it to a healthy plant.

3. Experimental transmission of kadang-kadang from diseased trees to healthy coconuts by means of insects, leafhoppers and related insects. There are at least 24 species, belonging to the genera *Cicadella Nisia, Makilingia,* etc.

4. Transmission of coconut kadang-kadang from coconut to various other species of palms. Among the palms being tested are *Areca catechu* and *Livistonia rotundifolia.*

5. Experimental transmission of coconut kadang-kadang from coconut to various species of weeds.

6. Transmission of kadang-kadang by mechanical means.

7. Spraying and dusting of diseased coconut trees to find out if the trees so treated recover.
8. Experimental control of the coconut "kadang-kadang". Object to determine effects of different treatments on the incidence of the disease.
    a. Cutting down diseased trees only.
    b. Cutting down and burning diseased trees.
    c. Spraying with insecticides and cutting diseased trees only.
    d. Spraying, cutting and burning diseased trees and keeping field free of vegetation.
9. Control of various coconut feeding insects with special reference to the use of insecticides.
10. Mechanical transmission of kadang-kadang.
11. Resistance studies.
12. Symptomatology studies.
13. Studies on microflora in relation to kadang-kadang.

Migratory Locust

1. Further studies on the biology, ecology and control of the Oriental Migratory Locust.

Coconut Pests

1. Further studies on the biology, ecology and control of the coconut black beetle, *Oryctes rhinoceros.*
2. Studies on mealy bugs on coconuts in relation to nut production.

Foot Rot of Kenaf

1. Studies on the control of foot rot of kenaf, caused by *Sclerotium rolfsii* and *Rhizoctonia solani.*

Coffee Rust

1. Further studies on the control of coffee rust, *Hemileia vastatrix.*

Powdery Mildew of Citrus

1. Studies on the powdery mildew of citrus and its control.

Giant snail

1. Further studies on the biology, ecology and control of the East African Giant Snail, *Achatina fulica.*

Cucurbit Leaf Beetle

1. Studies on the control of the cucurbit leaf beetle, *Ceratia similis.*

LITERATURE CITED

1. KOIDSUMI and OGASAHARA. 1940. The Philippine Locust and Its Relation to Taiwan (A climato-ecological consideration). *Journal of Tropical Agriculture,* Japan, 12, No. 4 (December).
2. OTANES, F. Q. 1925. Insects: Their Relation to Man and Their Control. *The Philippine Agricultural Review,* Vol. 18, No. 4: 373-410.
3. OTANES, F. Q. and A. G. TOQUERO. 1938. Further Observations on the Biology and Control of the Oriental Migratory Locust. *National Research Council of the Philippines Bulletin* No. 19: 109-110.
4. OTANES, F. Q. 1940. Notes on the Oriental Migratory Locust (*Locusta migratoria manilensis* Meyen) with Special Reference to Its Solitary Phase and Breeding Place or Outbreak Area. *The Phil. Journal of Agriculture,* Vol. 11, No. 4: 331-353.
5. UICHANCO, L. B. 1936. Secular Trends of Locust Outbreaks in the Philippines and Their Apparent Relation with Sunspot Cycles. *The Phil. Agriculturist,* Vol. 25: 321-366.
6. ————. 1937. A Biometrical Study of the Adult Component of Philippine Locust Swarms. *The Phil. Agriculturist,* Vol. 26: 237-289.
7. ————. 1938. A Progress Report on the Ecology of Probable Outbreak Centers of the Migratory Locust in the Philippines. *National Research Council of the Philippines Bulletin* No. 23 (December): 102-103.

Summary of Aerial Spraying by Five Planes in Masbate from September 3 to December 31, 1952

Month	PACO PIC—338				
	Total Solution Used in Gallons	Area or Size of Swarms Sprayed	Area Covered by Spray	Number of Flights	Number of Hours
September	8,488.10	1,816.0 F	1,551	145	101:50
October	6,990.50	1,178 F 8 H	1,080	119	100:00
November	6,185.83	353 F 194.5 H	967.5	112	123:20
December	585.75	13 F 11.1 H	91.0	10	8:25
Total	22,250.18	3,360 F 213.6 H	3,689.5	386	333:35

F—Flyers H—Hoppers

Month	CAA PL—33				
	Total Solution Used in Gallons	Area or Size of Swarms Sprayed	Area Covered by Spray	Number of Flights	Number of Hours
September	2,645.53	613 F	438	72	58:10
October	861.00	147 F 10 H	135	38	45:45
November	1,145.83	12 F 56.5 H	208	32	33:10
December	627.00	14.5 F 26.5 H	122	34	32:35
Total	5,279.36	786.5 F 93.0 H	903	176	169:40

F—Flyers H—Hoppers

Month	CAA L—32				
	Total Solution Used in Gallons	Area or Size of Swarms Sprayed	Area Covered by Spray	Number of Flights	Number of Hours
September	—	—	—	—	—
October	128.00	8	16	11	10:10
November	—	—	—	—	—
December	—	—	—	—	—
Total	128.00	8	16	11	10:10

F—Flyers H—Hoppers

	PAF—063				
MONTH	TOTAL SOLUTION USED IN GALLONS	AREA OR SIZE OF SWARMS SPRAYED	AREA COVERED BY SPRAY	NUMBER OF FLIGHTS	NUMBER OF HOURS
September	2,516.26	522 F	376	61	43:55
October	1,722.00	302 F	274	45	41:15
November	413.18	5 F	80	24	25:10
		36 H			
December	205.00	5.5 F	34	17	21:45
		5.0 H			
Total	4,856.44	834.5 F	764	147	
		41 H			132:05

F—Flyers H—Hoppers

	PAF—337				
MONTH	TOTAL SOLUTION USED IN GALLONS	AREA OR SIZE OF SWARMS SPRAYED	AREA COVERED BY SPRAY	NUMBER OF FLIGHTS	NUMBER OF HOURS
	1,355.56	381 F	239	34	24:40
October	2,536.80	501 F	445	67	68:35
November	1,979.58	113 F	334	53	56:30
		58 H			35:25
December	1,069.21	14.75 F	177	35	
		12.25 H			
Total	6,941.15	1,009.75 F	1,195	189	185:10
		70.25 H			

F—Flyers H—Hoppers

Explanations:

PACO PIC—338. Plane of the Philippine Airways Corporation. Hired by the Bureau of Plant Industry. The first plane to spray.

CAA PL—33 & CAA L—32. Planes loaned by the Civil Aeronautics Administration. Wages and traveling expenses and per diems of aviators paid by the Bureau of Plant Industry.

PAF—063 & PAF—337. Planes of the Philippine Air Force, Philippine Army. Loaned to the Bureau. Traveling and per diems of aviators paid by the Bureau.

ILLUSTRATIONS

PLATE I

FIG. 1.—A typical portion of Burias Island, Masbate, where swarms giving rise to the alarming 1952 locust outbreak originated.

FIG. 2.—Types of airplanes used in the locust campaign in Masbate: A, super cab and B, Philippine Airforce PT-13 (Big plane is C-47, a PAF supply plane).

PLATE II

FIG. 1.—Plane of the Philippine Airways Corporation in action against locust swarm in Masbate, September 3, 1953.

FIG. 2.—A portion of a pool in a creek showing locusts killed by airplane spraying with aldrin, September 3, 1953, at Malinta, Masbate, Masbate.

PLATE III

FIG. 1.—Airplane of the Civil Aeronautics Administration spraying a swarm with aldrin. A remarkable example of low, dangerous flying to spray swarms effectively.

FIG. 2.—A portion of a field in Masbate showing dead locusts killed by airplane spraying with aldrin.

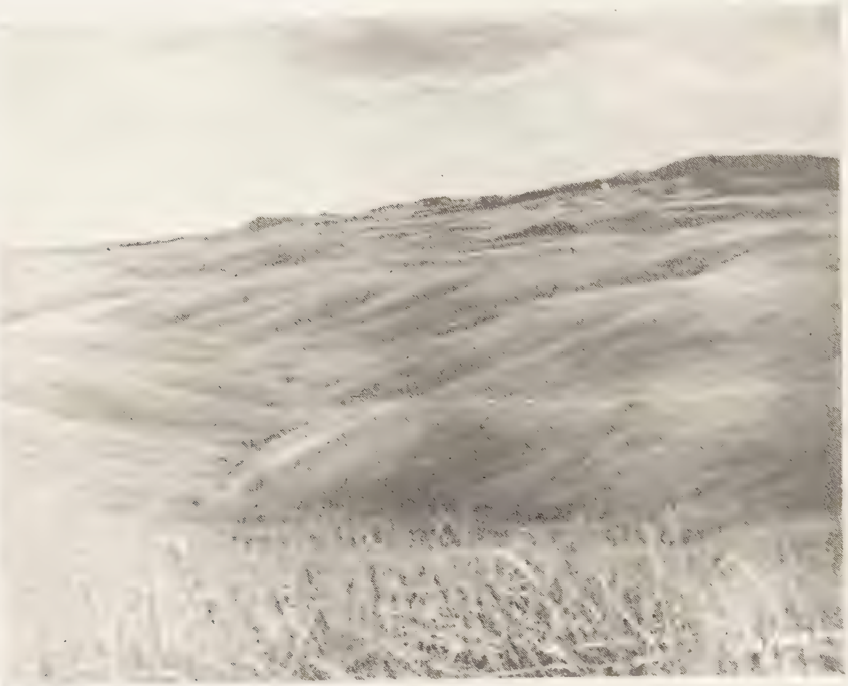


FIGURE 1

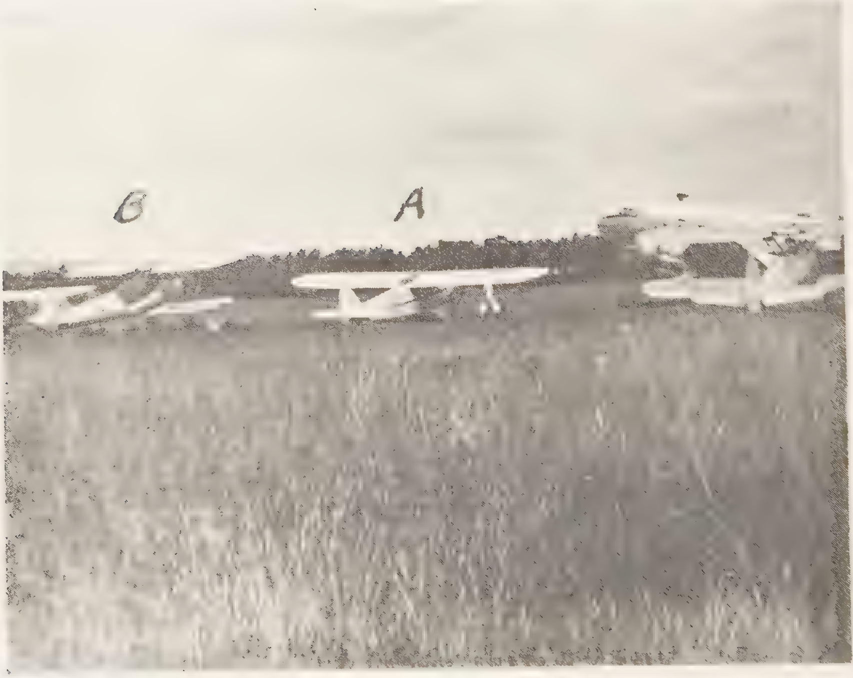


FIGURE 2

PLATE 1

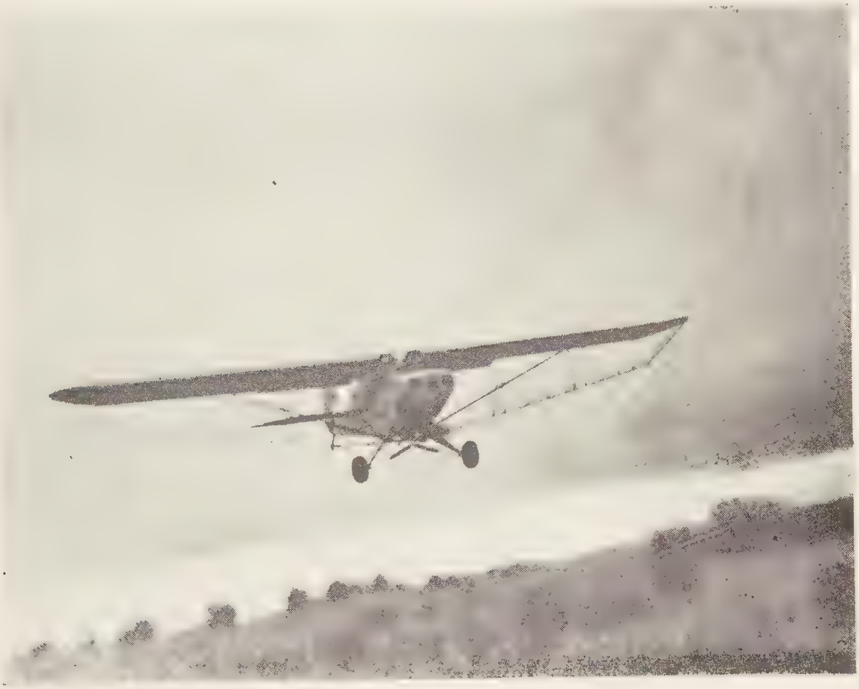


FIGURE 1

FIGURE 2

PLATE II

FIGURE 1

FIGURE 2

PLATE III

FURTHER STUDIES ON THE BIOLOGY, ECOLOGY AND CONTROL OF THE GIANT EAST AFRICAN SNAIL (*ACHATINA FULICA* FER.)

By Guillermo A. Pangga
Entomology Section, Plant Pest and Disease Control Division
Bureau of Plant Industry, Manila, Philippines

INTRODUCTION

In 1949 the writer published a preliminary paper on the biology, ecology and control of the Giant African Snail (*Achatina fulica* Fer.). Since then additional data have been obtained and are reported in the present paper. The snails are destructive especially to vegetables and ornamental plants.

During the last five years numerous complaints have been received regarding the destruction caused by snails on vegetables and truck crops not only in Manila but also in some provinces. In some places in Cavite and Rizal, the growing of beans has become unproductive because of the snails.

History and Distribution

According to Williams (1949) the Giant East African Snail is a native of the lowlands of tropical East Africa, including the Zanzibar Islands. It is said that during the past hundred years or more the snail has found its way into most of the tropical islands along the Indian and Pacific Oceans.

Williams (1949) reports that a record dated about 1857 speaks of an enthusiastic malacologist who took some to Calcutta for purposes of dissection. According to the same author, great damages by the snails were reported to Ceylon in 1910, Malaya in 1923, Singapore in 1928, and Hawaii in 1938. The Japanese spread the snails throughout their mandated Islands in Micronesia. These snails are also known to be present in Java, Borneo, Amoy (China), and Formosa. It is said that snails succeeded in entering the United States, through jeeps, tires, pipes and other surplus equipment on scrap metal shipped back from the Pacific Islands. Because of the prompt and rigid action taken by the United States plant pest and disease control services, it appears that the threat of the Giant Snail establishing itself in California has been cut short.

Giant snails were presumably brought into the Philippines by the Japanese Army in 1942, for multiplication to be used as food, although it is claimed in some quarters that specimens had been collected in Pasay, Rizal, before the war. The snails have spread to other provinces through the agency of the Japanese soldiers who might have carried them also for food as they moved from place to place. Some individuals working in Japanese firms in Manila upon returning to their respective homes in the provinces, might have brought with them some snails either for food or as toys or playthings for their children.

The snails are found almost everywhere in Manila and suburbs. Now the snails are found in the provinces of Agusan, Albay, Batangas, Bulacan, Camarines Sur, Camarines Norte, Cavite, Cebu, Iloilo, Laguna, La Union, Misamis Oriental, Misamis Occidental, Nueva Ecija, Nueva Vizcaya, Negros Oriental, Pampanga, Quezon and Rizal.

FOOD PLANTS

The snails are polyphagous. Among the vegetables, cabbage, *Brassica oleraceae* L. var. *capitata* Hort. and pechay, *Brassica cernua* F. and H. seem to be the favorite host plants. Among the field crops, cucumber, *Cucumis sativus* L., squash, *Cucurbita maxima* Dch., gabi, *Colocasia esculenta* Sct., ampalaya, *Momordica charantia* L., *patola, Luffa acutangula* R x b., *Luffa cylindrica* Noem., upo, *Lagenaria leucantha* Rby., okra, *Abelmoschus esculentus* L., ubi, *Dioscorea alata* L., mongo, *Phaseolus aureus* R x b., cowpea, *Vigna sinensis* Savi., and sitao, *Vigna sinensis* var. *sesquipedalis* Fruw., are seriously attacked. The snails have also been observed to attack coffee, *Coffea* sp., chico, *Achras zapota* L., lanzon, *Lansium domesticum* J., canna, *Canna indica* L., *Philodendron* sp., Doña Aurora, *Mussaenda philippica* var. *Doña Aurora,* eggplant, *Solanum melongena* L., cassava, *Manihot utilissima* Pohl., malungay, *Moringa oleifera* Lam., *Colopogonium coerrolum, Pueraria javanica,* papaya, *Carica papaya* L., pepper, *Capsicum annum* L., black pepper, *Piper nigrum* L., nangka, *Artocarpus integra* M., banana, *Musa sapientum* L., mulberry, *Morus alba* L., cosmos, *Cosmus bipinatus* L., marigold, *Tagetes erecta* L., rose, *Rosa* sp., ramie, *Boehmeria nivea* (L.) Gaudich., gumamela, *Hibiscus rosea-sinensis* L., sweet potato, *Ipomoea batatas* L., zinnia, *Zinnia elegans* and dilang-baka, *Nopalea cochinellifera* (L.) Salm, Dyck. It was found, however, that plots of onions and lettuce in the Central Experiment Station were not damaged by the snails. Otanes (1948) reported it as one of the pests of orchids, especially *Phalaenopsis.* At night the snails are commonly found feeding on garbage piles. They also feed on decaying vegetables, banana peelings, rind of water-melon, decaying tomatoes, papaya fruits, chicken feces and even human feces. They have also been observed to feed on the flesh of crushed snails of their own kind. They destroy citrus by gnawing the bark. In Java it was reported by Kalshoven and Van der Vetcht (1950) that in old Hevea plantations the snails have been found to feed on coagulated as well as flowing latex and they ingest this in relatively large quantities.

Thick cardboard paper inside breeding cages was almost completely eaten when the snails were starved.

Observations in the field showed that rice plants were not damaged by the snails although they were present in relatively large numbers in rice paddies.

In general the attack is most frequent on young host plants. It is in the early growth of the plants that the most serious injury occurs. Young plants just shooting through the ground are very susceptible. Infested plants can be detected even before the snails are seen because of the riddled appearance of foliage (Plate II, Fig. 1).

DESCRIPTION

The body of a snail consists of the head, neck, visceral hump and foot. The body is usually soft, light gray to dark gray, and when fully extended, it measures from 6 to 9 centimeters long (Plate I, Fig. 7). The head is provided with two pairs of retractile tentacles. The eyes are located at the extremities of the upper tentacles. The lower pair of tentacles are shorter, and they probably bear the sense organs of touch and smell. The mouth is surrounded by fleshy lips and below it is the opening of the slime gland. On the right side of the mantle is the breathing pore and back of this is the anus. On the upper part of the mouth is a sharp cutting mandible. The genital aperture is on the right side of the body near the head. The snail moves along by an undulating movement of the muscles of the foot over a slippery track of mucous, secreted by glands in the foot while the snail is in motion. This silvery-like trail that the snail leaves wherever it goes is the mucous substance which solidifies on exposure to the air. When disturbed it withdraws the entire body into the shell.

Full grown shells have from 6 to 7 whorls (Plate I, Fig. 7). The shell is that of dextral or right hand spiral. The length of the shell was found to vary from 8 to 10 centimeters. The first and largest whorl is of chestnut brown color with longitudinal bands of light brown and yellow. The second and third whorls from above are chestnut brown color with wavy bands of yellow. The other whorls—the fifth, sixth and seventh—are brown with longitudinal bands of light brown.

Life History & Habits

In the early stages of the work on the life history of the snail, many points concerning its habits etc., had to be determined in order that surroundings nearly as normal as possible might be provided. Much of the work had been carried outdoors where snails were placed on moist soil in separate cages. The food given to the snail consisted of decaying organic materials and fresh leaves of pechay, beans, hibiscus, etc. For the supply of calcium, fresh leaves given to the snail were dusted with ground shell (powder).

These snails are hermaphroditic. In outdoor cages where pairs of snails were reared, pairing usually took place during night and most often the process was not completed before daybreak so that snails were often seen in coition in the morning. Oviposition occurred from 12 to 28 days after mating.

Preparatory to laying, the snails buried themselves in the soil forming a round dugout below. It took from 24 to 48 hours for the snails to deposit the eggs. When each snail had finished oviposition it closed the opening of the burrow or nest. In the field, however, the snails were observed to lay eggs under piles of trashes and hedges, stone crevices, or just below or on the surface of the soil in shaded places (Plate III, Fig. 1). Field observations have shown that snails began to lay eggs as early as May and laying continued up to November. Most of the snails laid their eggs in July and August. The eggs were laid one by one in a loose mass. They are oval, about 4 to 5 millimeters in diameter, and with a hard shell (Plate I, Fig. 1). At first the eggs are light yellow but as the time of hatching approaches they turn white. The eggs hatched in 5 to 15 days. Snails reared from eggs in outdoor cages were found to lay from 78 to 142 eggs (Table II). Mature snails, however, collected from the field and put in battery jars laid from 198 to 305 eggs (Table III). In most cases, however, snails laid eggs when they were from 254 to 375 days old. One snail was found to lay eggs when it was 425 days old.

The newly hatched snail is provided with a shell of two whorls, the shell being milky white, brittle and transparent. (Plate I, Fig. 2). The young snails usually remained three to four days in the nest before they came out in search for food. A young snail that has a broken shell can mend it easily. A considerable number of young snails died from natural causes. Others are attacked by red ants, *Solenopsis geminata* Fabr., before they become fully developed.

Observations in the field showed that young snails are gregarious and hundreds of them can be found on a single plant. When they are about two months old (Plate I, Fig. 5) they disperse to the other plants.

Snails from 254 to 425 days old began to lay eggs and lived from 303 to 455 days (Table I). According to Kalshoven and Van der Vetcht (1950), the snails could live from 2½ to 3 years. According to South (1926) the snails probably took two years to attain their full size, but are capable of laying eggs at the end of the first year when half grown. There is only one generation in a year.

They are typically nocturnal in habit and the majority of their activities are carried on at night. During the day they conceal themselves in shady and moist places, under stones, in cracks and crevices, in buildings and other hiding places. They can also be found resting on trunks of trees especially bananas, and papayas, and stone walls (Plate IV, Fig. 1) and on hanging dried leaves.

In the even climate of Malaya, according to South (1926), the snails appeared to be active throughout the year in suitable localities, although resting snails were found in rather dry places of Singapore in June after a long spell of dry weather. In the Philippines, the giant snail is most active during the wet or rainy season. During the dry season, most of the snails buried themselves in loose soil or hid under wood or stone piles, compost piles, and closed the opening of its shell with parchment-like cover. They aestivated or remained inactive for many days. However, in gardens that are regularly watered, the snails are always active or do not aestivate. It was found that the snails remained inactive from 95 to 120 days. This inactivity induced by dryness appears to be a temporary protection for the snails against adverse external conditions. When favorable conditions prevail as when the rainy season sets in they come out of their hiding places and resume their normal activity.

Natural Enemies

From the dead snails, different kinds of flies emerged, belonging to the family Phoridae, Phychodidae, Ephydridae, Muscidae and Sarcophagidae. All these flies were of the non-parasitic type. The first three are common on decaying organic matter and the last two are common flesh flies. Newly hatched snails and even the mature ones were observed attacked by red ants, *Solenopsis geminata* Fabr.

Control Measures

Hand-Picking

During the Japanese occupation when hunger and misery were prevalent, people collected the snails for food. The snails were even sold in Manila markets.

After liberation when there was no control measure known, the snails were collected by hand and destroyed either by crushing and burying them in the soil or burning them. Although this method is laborious, it is very effective. School children can be employed to great advantage. Since the smaller snails are usually missed, the collection should be done as often as possible. There are persons, however, who collect the snails, boil and chop them into pieces for hog feed. This will help minimize their numbers.

Traps and barriers

Certain materials were tested in an effort to find some objects on or under which snails will congregate to conceal themselves when they leave the plants. Later these traps were examined and snails found were destroyed. The materials used were gunny sack, dried leaves and twigs. These were placed along the fences and in places where snails were usually abundant. It was found that from 65 to 408 snails could be collected from piles of dried twigs and leaves. From gunny sack 16 to 166 snails could be collected (Table IV). It was found, however, that piles of dried leaves and twigs served as better traps for snails than pieces of gunny sack, because the soil beneath the piles of dried twigs and leaves tended to remain moist while beneath the gunny sack it tended to dry out.

Certain deterrent dusts and substances such as hydrated lime, tobacco dust and common table salt to prevent snails from entering uninfested vegetable plots, were tested.

In the laboratory, groups of snails are surrounded with these substances and the results are shown in Table V. It was noted that snails surrounded with a band or barrier of hydrated lime failed to cross the bands and later closed the opening of their shell and aestivated. Those surrounded with tobacco dust, failed to cross the band and when the body was coated with dust, the snails looked apparently dead and could not withdraw their bodies into the shell. However, snails that stuck to the band of salt died after 24 hours and others after 36 hours.

In the field, tests were made in the Entomology experimental plots and other plots in the Central Experimental Station planted to vegetables.

Hydrated lime, tobacco dust and common table salt were applied in bands, 2 inches wide and ½ inch thick, 30 cm. away from the plot. Then freshly collected snails were placed near the plots surrounded by these substances. The results are shown in Table VI. It will be noted that the plants in the plots surrounded with a band of hydrated lime were not destroyed. The snails were deterred on the band of lime. The same result was obtained in case of plots surrounded by bands of tobacco dust and common table salt. All plants in the check plots were damaged by the snails. In case of tobacco dust, when the body of the snail was coated with dust for 5 days, the snails eventually died. However, salt did not only prevent the snails from entering the uninfested plots but also killed the snails by dehydration. Viado (1950) reported that bamboo halves of lengths suitable for the purpose buried in the ground up to the rim have been found satisfactory containers or troughs for the salt. "These receptacles also serve as traps. When this kind of trough was used it was found that saturated salt solution was more effective than the crystals as shown by more snails and slugs caught in the trough when solution was used."

At present there are several individuals using salt in controlling the snails in their premises. The only setback in using hydrated lime, tobacco dust and salt in the field, is that it cannot be done during the rainy days.

Poisoned baits

As a result of several tests made rice bran containing 5 per cent metaldehyde and made moderately moist with water is now employed as standard bait against the snail. There has been no doubt raised, so far, by persons supplied with baits as to the effectiveness of the bait. The baits proved very attractive to snails and slugs and large numbers could be killed in this way in a short period (Plate V, Fig. 1 & Plate VI, Fig. 1). Baits containing 5 per cent calcium arsenate and 2 per cent metaldehyde in rice bran were also tested in the field and have been found also effective against this snail. In the absence of rice bran, sawdust may be substituted.

The advantage of sawdust over rice bran is that sawdust can be obtained free from local sawmills. Also it does not get moldy easily when wet and the chickens do not touch sawdust unlike the rice bran.

SUMMARY

1. The Giant East African Snail (*Achatina fulica* Fer.) is a native of East Africa. From Africa it has spread to other parts of the world, the Philippines included, through the agency of man.

2. The snail is a serious pest of vegetables, ornamentals and fruit crops.

3. Young plants are most seriously damaged, although plants in all stages of development are attacked.

4. The host plants include a large number of species preferably cabbage, *Brassica oleracea* L., var. *capitata,* pechay, *Brassica cernua* F. & H., cucumber, *Cucumis sativus* L., squash, *Cucurbita maxima* Dch., gabi, *Colocasia esculenta* Sct., ampalaya, *Momordica charantia* L., patola,

Luffa acutangula R x b., *Luffa cylindrica* Noem; upo, *Lagenaria leucantha* Rby., okra, *Abelmoschus esculentus* L., ubi, *Dioscorea alata* L., canna, *Canna indica* L., *Philodendron* sp., Doña Aurora, *Mussaenda philipica* var. *Doña Aurora*, mongo, *Phaseolus aureus* R x b., cowpea, *Vigna sinensis* Savi., sitao, *Vigna sinensis* var. *sesquipedalis* Fruw., coffee, *Coffea* sp., chico, *Achras zapota* L., lanzon, *Lansium domesticum* J., eggplant, *Solanum melongena* L., cassava, *Manihot utilissima* Pohl., malungay, *Moringa oleifera* Lam., *Colopogonium coerrolum*, *Pueraria javanica*, papaya, *Carica papaya* L., pepper, *Capsicum annum* L., black pepper, *Piper nigrum* L., nangka, *Artocarpus integra* M., banana, *Musa sapientum* L., mulberry, *Morus alba* L., cosmos, *Cosmus bipinatus.*, *sapientum* L., mulberry, *Morus alba* L., cosmos, *Cosmus bipinatus* L., Gaudich, gumamela, *Hibiscus rosea-sinensis* L., sweet potato, *Ipomoea batatas* L., zinnia, *Zinnia elegans*, dilang-baka, *Nopalea cochinellifera* (L.) Salm. Dyck., *Citrus* sp., and orchid, *Phalaenopsis* sp.

5. The snail is typically nocturnal in habit.

6. The snail is most active during the wet or rainy season and remains inactive during the dry season.

7. It was found that the snails remained inactive between 95 and 120 days.

8. The snail is hermaphroditic.

9. The eggs are deposited about one inch deep in the soil. In the field the eggs were laid under piles of trashes and hedges, stone crevices, or just below or on the surface of the soil in shaded places.

10. Records of the number of eggs laid by one snail reared from eggs varied from 78 to 142 eggs. Mature snails, however, collected from the field and put in breeding cages laid from 198 to 305 eggs.

11. The incubation period of the eggs varied from 5 to 15 days with an average of 9.34 days.

12. Snails began to lay eggs from 254 to 425 days old with an average of 323.58 days.

13. Oviposition occurred from 12 to 28 days after mating.

14. The snails lived from 303 to 455 days with an average of 388.42 days.

15. The complete life cycle (from egg to egg laying) ranged from 266 to 437 days with an average of 337.5 days.

16. In a small garden the snails can be collected by hand and destroyed either by crushing and then burying them or by burning them.

17. Moistened old gunny sacks, twigs and leaves of trees placed where snails were numerous were observed to be good traps for snails.

18. The use of tobacco dust, hydrated lime and common table salt may help in preventing snails from entering uninfested areas. How-

ever, common table salt does not only prevent the snails but also kills them.

19. Snails can be effectively controlled by baits containing 5 percent metaldehyde in rice bran and set one to two meters apart.

20. There was no parasite on the snail observed so far. At times, however, newly hatched snails and even the mature ones were observed to be attacked by red ants, *Solenopsis geminata* Fabr.

LITERATURE CITED

1. BASIGNER, A. J. 1931. The European brown snail. *Univ. of Calif. Agri. Expt. Sta. Bull.* 515: 2-20.
2. CORBETT, G. H. 1938. The giant snail (*Achatina fulica* Fer.) *The Malayan Agri. Journ.* 26(6): 376-379, figs. 1-2.
3. GUNN, D. 1924. The brown and gray snails. Two destructive garden pests. Union of South Africa. (Reprinted from the *Journ. of Dept. of Agri.* 48:2-10).
4. HELY, P. C. 1946. Control of snails on citrus trees. *The Agricultural Gazette.* 57(5): 239-245.
5. LEWI, K. C. and J. R. FOLLETE. 1942. Control of the brown snail in citrus orchard. *Journ. Eco. Ent.* 35(3): 359-362.
6. KALSHOWVEN, L. G. E. and J. VAN DER VETCHT. 1950. De Plagen Van de Cultuurgewasen in Indonesia. I. 512 pp. N.V. Uitgeveris W. Van Hoeve. S. Gravenhage Bandoeng.
7. OTANES, F. Q. 1948. Notes on orchid pests and suggestions for their control. *Phil. Orchid Review.* 1(1): 12-18, 1 plate.
8. PANGGA, G. A. 1949. A preliminary report on the biology, ecology and control of the giant African snail (*Achatina fulica* Fer.) *The Phil. Jour. of Agri.* 14(4): 337-347, 1 plate.
9. SOUTH, F. W. 1926. The giant snail (*Achatina fulica* Fer.) in Malaya. *The Malayan Agri. Jour.* 14(17): 231-241.
10. VIADO, G. B. 1950. Control of land snails and slugs. *Agricultural and Industrial Life.* 12(11): 4-5, 37.
11. WILLIAMS, L. C. 1949. Enlightened Africa. (Reprinted from the *Scientific Monthly.* 68(3): 199-207).

TABLE I

Summary of the Life History of the Snails from July 1948 to December 1952.

Stage	No. of Individuals	Range (days)	Average (days)
Incubation period of eggs	48	5–15	9.34
Emergence of snail to oviposition	24	254–425	323.58
Mating to oviposition	14	12–28	16.75
Number of eggs laid by a snail	24	78–142	118.12
Life cycle (from egg to egg laying)	24	266–437	332.5
Longevity	24	303–455	388.42
Number of generations annually			1

TABLE II

Number of Eggs Laid by Snails Reared in Cages (From Egg to Egg Laying)

Date	No. of Eggs	Date	No. of Eggs
17 — VI 1949	132	2 — X 1950	114
28 — VI 1949	130	24 — X 1950	140
21 — VII 1949	119	4 — V 1951	78
15 — VIII 1949	110	2 — VI 1951	134
5 — IX 1949	137	25 — VII 1951	139
5 — XI 1949	98	24 — VIII 1951	125
12 — VI 1950	108	27 — VIII 1951	87
16 — VI 1950	94	27 — IX 1951	116
20 — VI 1950	106	11 — X 1951	135
3 — VII 1950	112	22 — X 1951	129
6 — VII 1950	138	8 — XI 1951	89
30 — VIII 1950	122	19 — XI 1951	142

TABLE III

Number of Eggs Laid by Mature Snails Collected from the Field

Date	Number of Eggs	Date	Number of Eggs
21 — VI 1947	198	20 — VIII 1948	218
16 — VI 1947	265	10 — IX 1948	280
19 — VI 1947	281	18 — IX 1948	233
9 — VIII 1947	251	24 — IX 1948	269
17 — VIII 1947	305	29 — IX 1948	243
10 — IX 1947	196	6 — VIII 1949	298
2 — IX 1947	230	14 — VIII 1949	283
24 — X 1947	215	19 — VIII 1949	266
29 — IX 1947	205	25 — VIII 1949	257
2 — VII 1948	212	3 — IX 1949	288
12 — VII 1948	265	7 — IX 1949	264
24 — VII 1948	296	26 — IX 1949	239
27 — VII 1948	268	11 — IX 1949	278
8 — VIII 1948	288	7 — XI 1950	274
10 — VIII 1948	266	8 — XI 1950	202
22 — VIII 1948	301	18 — XI 1950	219

TABLE IV
NUMBER OF SNAILS FOUND UNDER PILES OF DRIED TWIGS, LEAVES AND GUNNY SACK.

Material	Date Applied	Treatment	Date Examined & Number of Snails Found						Remarks
			June 2 1952	July 7 1952	Aug. 4 1951	Sept. 1 1951	Oct. 6 1951	Nov. 3 1951	
Dried twigs and leaves	5–V–1951	5 piles of dried twigs and leaves	65	202	408	185	93	48	More attractive because it tended to remain moist
Gunny sack	5–V–1951	5 pieces of gunny sack	29	144	166	121	36	16	Tended to dry out

TABLE V
EFFECT OF HYDRATED LIME, TOBACCO DUST AND SALT WHEN APPLIED AS BAND AROUND THE SNAILS.

Material	Date Applied	Treatment	Effect on Snails
Hydrated lime	8–I–52	As 2-inch band on the soil around 25 snails	Snails failed to cross the band. All closed the opening of the shell and aestivated.
Tobacco dust	8–I–52	As 2-inch band on the soil around 25 snails	Bodies of snails coated with dust could not withdraw inside the shell. 9 snails died after five days.
Salt	8–I–52	As 2-inch band around 25 snails	Snails failed to cross the band. After 24 hours 6 snails died and others were sickly and closed the opening of the shell. After 36 hours another 12 snails died.

TABLE VI

Effect of Hydrated Lime, Tobacco Dust and Salt when Applied in the Field around Vegetable Plots.

Materials	Date of Application	No. of Trials	Method of Application	Mean No. of Snails around Plots	Effect on Plants	Remarks
Hydrated lime	14–I–1952	5	As 2-inch band around 1 plot (1 m. × 5 m.) of pechay, 30 cm. from the bed.	56	plants not damaged	30 snails stuck on the band and failed to enter the plots.
Check	14–I–1952	5	1 plot (1 m. × 5 m.) of pechay	56	plants seriously damaged	
Tobacco dust	14–I–1952	5	As 2-inch band around 2 rows of cucumber (156 plants), 30 cm. from the row	45	plants not damaged	26 snails stuck on the band. Failed to enter the rows of cucumber.
Check	14–I–1952	5	1 row cucumber (55 plants)	45	plants seriously damaged	
Salt	21–I–1952	5	As 2-inch band around 1 plot (1 m. × 5 m.) of pechay, 30 cm. from the bed.	52	plants not damaged	30 snails stuck on the band and failed to enter the vegetable plot.
Check	21–I–1952	5	1 plot (1 m. × 5 m.) of pechay	52	plants seriously damaged	

ILLUSTRATIONS

PLATE I

Fig. 1.—Egg (natural size).
Fig. 2.—Newly hatched snail (natural size).
Fig. 3.—Young snail, 2 weeks old (natural size).
Fig. 4.—Young snail, 1 month old (natural size).
Fig. 5.—Young snail, 2 months old (natural size).
Fig. 6.—Snail about 1 year old (natural size).
Fig. 7.—Fullgrown snail body partly out of the shell (natural size).

PLATE II

Fig. 1.—Snails feeding on mulberry leaves.

PLATE III

Fig. 1.—Eggs laid on the surface of the soil (natural size).

PLATE IV

Fig. 1.—Young and mature snails clinging on stone wall and on piles of dried twigs.

PLATE V

Fig. 1.—Piles of dead snails on metaldehyde bait.

PLATE VI

Fig. 1.—A closer view of another pile of dead snails on metaldehyde bait.

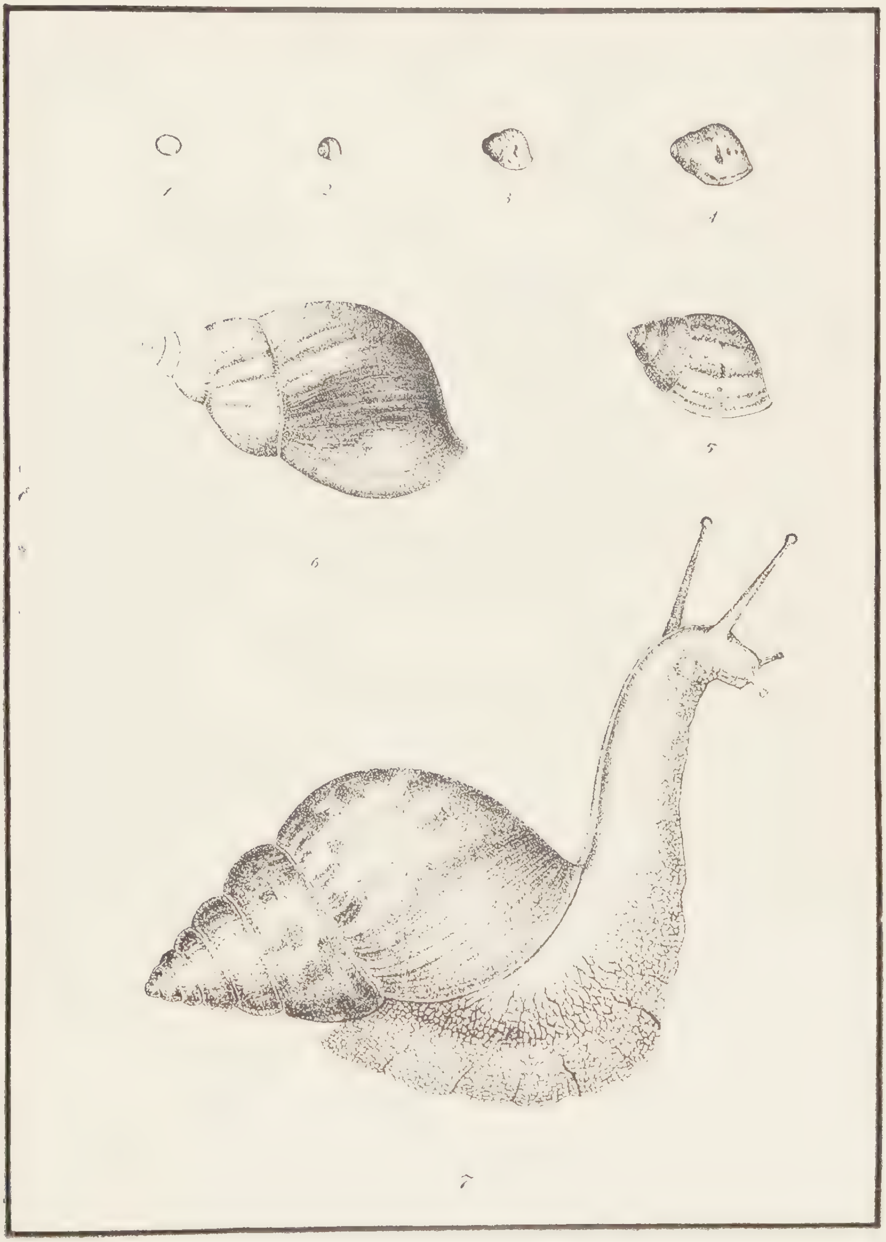


PLATE I

PLATE II

PLATE III

PLATE IV

PLATE V

PLATE VI

THE INSECT FAUNA OF MICRONESIA

By J. Linsley Gressitt
Bishop Museum, Honolulu, Hawaii

The insect fauna of Micronesia is the subject of a rather extensive project being undertaken at the Bishop Museum with the cooperation of several other museums or universities and the participation of a large number of specialists. This undertaking is largely the result of collaboration between the Pacific Science Board of the National Research Council in Washington, the Bishop Museum, the Trust Territory of the Pacific Islands, the Office of Naval Research, and other organizations. At the beginning of 1953 the project was transferred from the Pacific Science Board to the Bishop Museum, and the museum received a grant from the National Science Foundation in Washington to help support the undertaking.

Since 1948 the Pacific Science Board has sent out nearly 20 American entomologists to Micronesia, some of them on pest surveys and others to make systematic collections in the different island groups. Some of these collections were mounted at the Chicago Natural History Museum, the Museum of Comparative Zoology (Harvard University), the California Academy of Sciences, and the University of California. The work is being completed at the Bishop Museum. A number of other collections, made during, or just after, World War II are also being used in the study. Many of these were at the U. S. National Museum, at the Chicago Natural History Museum and at the California Academy of Sciences. Some pre-war collections from Guam and the Caroline Islands were already at the Bishop Museum and the Hawaiian Sugar Planters' Association Experiment Station. Prof. T. Esaki of Kyushu University, Japan, is cooperating by submitting his unstudied Micronesian collections.

These combined collections total well over 400,000 specimens of perhaps 5,000 species. All terrestrial arthropods are to be included in the study. Over 100 specialists have now agreed to collaborate on the project and the material is being distributed to them. These workers represent about 50 institutions in 13 countries. The results of these studies will be published by the Bishop Museum as a series under the title "Insects of Micronesia."

Micronesia is a remarkable assemblage of over 2,000 islands spread over the western Pacific Ocean, mostly north of the equator. Most of the islands are very small, and the largest, Guam is only 50 km. long. The territory includes the Mariana, Caroline, Marshall and Gilbert Islands, with also Ocean, Nauru, Wake, Marcus and the Bonin and Volcano Islands included in the scope of the study. Micronesia includes islands of several types, particularly volcanic islands, others of greatly raised coral limestone, atolls and raised atolls. The former two types are called 'high' islands and the latter two 'low' islands. Some of the 'high' islands consist of a combination of igneous and coral rock. The 'low' islands include the world's two largest atolls and the second largest assemblage of atolls. Truk, in the center of Micronesia, is the largest 'almost atoll', and is the much eroded remains of a large volcano. The volcanoes of western Micronesia are west of the 'sial' or 'andesite line' and extrude andesite, while those east of the line consist of basalt. The latter include Truk, Ponape and Kusaie. Of the former, the southern Marianas and the southern Palaus consist largely of raised limestone, and the Bonins, Volcano Islands and northern Marianas include the only active volcanoes. Yap and the northern half of the Palaus are much more complicated geologically than the other islands, and are much more ancient, possessing various metamorphic rocks. They also possess the richest insect faunas, and have even been called continental islands by some workers. However, they lack many important families or tribes of insects which are well represented in the nearby continental islands such as the Philippines and New Guinea.

The insect faunas of the principal groups of high islands are much richer than those of the low islands and of the small volcanic islands. The insect fauna of Guam, for instance, may number 2,000 species, and that of the Palaus perhaps twice that much. In the case of atolls the maximum may be in the neighborhood of 1,000 species, and only that much in the case of large humid atolls in the western Carolines, like Ulithi, or an atoll very near a major high island, like Kayangel in the Palaus. More isolated, or drier, atolls may have only about 500, or far fewer, species.

The faunas of the various atolls, even of widely separated ones, are not very different in makeup. This suggests that because of their similar, and limited, floral and ecological setting, they can only support a limited number of insect types, and also that the sources of their faunas are more or less in common. The faunas of the various high island groups, however, are distinctive and show both the results of speciation through isolation and varying ecological setting, and somewhat different origins of their faunas. The comparisons are not entirely equivalent, since there are no low islands in the Marianas, Volcano Islands or Bonins, and no high islands in the Marshalls or Gilberts. Thus only the Carolines possess both categories of islands.

Though it is too early in this study to draw conclusions, it seems evident that the insect fauna of Micronesia has been derived from various sources and by various means. Important sources appear to be the Philippines, particularly for Palau, Yap and Guam; eastern Indonesia, particularly for the western Carolines (Palau and Yap); New Guinea, for the Carolines in general; Polynesia, for eastern Micronesia; and Japan, for the Bonins and Volcano Islands, and to a lesser extent the Marianas.

As to the means by which the insects reached these islands, assuming they are all oceanic islands, air currents, storms and ocean currents have probably played a great part, exclusive of the activities of man. The types of insects can be roughly classified according to the probable methods of their reaching the islands. A large number, such as cockroaches, ants, pests of stored food or human clothing or implements, such as borers of dead wood, and others such as certain flies, mosquitoes, fleas, bed-bugs, lice, mites and ticks, may very likely have been brought by human agency. Others, probably a very small minority, may have been brought accidentally by migrating or strayed birds. Then, probably the predominant group, are those carried by air currents and storms. Dominant, again, among these are small insects of many types, but particularly those of low specific gravity and not too fragile nature, such as small flies, true bugs, leaf hoppers and their relatives, bees, small moths and some beetles. The last group, those carried in floating trees or logs by ocean currents, is probably much more limited, and perhaps largely restricted to beetles which live in wood at some stage in their development.

Thus the insect species of Micronesia are largely small in size, and among the dominant groups are small beetles and other insects which live in vegetation, small moths, and other inconspicuous forms. Large and showy insects are extremely few in number of species. It would appear probable that many of those present might have been carried by strong winds from the nearby continental islands. It is now known that at moderately high altitudes strong air currents exist which have high velocities and rather regular patterns. Though most of these air currents today are not directed towards Micronesia from areas rich in insects, it is true that the directions of these currents change with evolving climate and have been different in the past, and also that erratic storms may take any direction.

Micronesia is not as isolated as are the Hawaiian Islands, the Marquesas or some other oceanic islands and therefore undoubtedly have more frequent natural introductions of insects. Thus the number of ancestral types is greater and many more families of insects are represented. Also, the same species may be repeatedly introduced, and the influx of genus from similar parents populations may reduce the rate of speciation. It is interesting that certain genera are widespread in the different island groups, often possessing very closely related populations on different groups, while other related genera on the neighboring continental islands are totally lacking. This may suggest spread from one island group to another within Micronesia, or it might mean that certain types of insects are less easily carried into the upper air or by storms, or have greater difficulty in establishing themselves on oceanic islands.

As to relative endemicity in the different island groups, this can only be guessed at this stage. Possibly the percentage of endemics is over 60% for Palau and Ponape, with a lower rate for most of the other groups. Yap has quite a bit in common with Palau, but is much poorer. Truk has some interesting endemics, and some groups not found in the other islands, but in general it is much poorer than Palau, Guam or Ponape. Ponape appears to have the greatest number of endemic genera. Kusaie has many endemics, but they are often closely related to forms on Ponape. As suggested above, the atolls are poor in endemics. Many of their species are possessed in common with western Polynesia.

Summarizing, the insect fauna of Micronesia is a composite of several faunas and not an even cross-section of the insect world. It seems to be the result of selective processes controlling the transport of insects to the various islands, and the survival of the insects on the islands which they reach. Speciation has been taking place, but not to the extent known to occur on more isolated islands.

STATUS OF TERRESTRIAL MALACOLOGICAL RESEARCH IN THE CENTRAL PACIFIC AND MICRONESIA

By Yoshio Kondo
Bernice P. Bishop Museum, Honolulu, Hawaii

Introduction

By the old method of enumeration, there are fifteen land molluscan groups characterizing the Inner Pacific area. These are: Rhytididae (Paryphantidae), Zonitidae, Endodontidae, Achatinidae (Stenogyridae), Succineidae, Bulimulidae, Partulidae, Pupillidae, Tornatellinidae, Achatinellidae, Amastridae, Cyclophorodae, Assimineidae, Helicinidae, and Hydrocinidae. Of these fifteen, four groups are endemic to the Inner Pacific, namely, Partulidae, Tornatellinidae, Achatinellidae, and Amastridae. This means that these named four groups are to be found nowhere in the world excepting in the Inner Pacific, and it has been the opinion of malacologists that their origin is presumably within this area itself. This opinion is naturally subject to change as time goes on and more research is accomplished.

Land molluscan research consists of two phases, namely, (1) a systematic collection of the mollusks of each island group and (2) study of the collections in the laboratory and the publication of results. It might be said that both phases have been progressing at a snail's pace, but a certain amount of advancement has been made within the last 20 years. It might also be added here that, while much systematic collection remains to be accomplished, its implementation depends largely upon financial support which is largely non-existent at the present time.

Systematic Collections

In recent years, several major expeditions have explored the islands of the Pacific for their land molluscan fauna. The Bishop Museum's Mangarevan Expedition of 1934 to the Tuamotu, Austral, and Society Islands collected a rich series of endemic land shells. In 1936 another expedition into the Caroline Islands accumulated on excellent collection of land molluscs. The Lau Islands and some of the larger islands of the Fiji Group were explored in 1938.

Through previous non-molluscan expeditions, some idea of the shell fauna of the following islands have been derived: Cook, Tonga, Marquesas, New Hebrides, Solomons, Bismarck, Juan Fernandez, and the numerous atolls of the Pacific.

Hawaii is naturally well worked though much remains to be done in those islands beyond Oahu. Samoa has been collected systematically by Cooke, Zimmerman, and Harris. The Marianas has been subject to collections by several expeditions.

A tabular summary is given on the last page of this report summarizing the approximate percentage of completion in collecting for each island or each group of islands.

Systematic Research

In the Introduction it was stated that the Inner Pacific is characterized by the four endemic land molluscan groups Partulidae, Amastridae, Tornatellinidae, and Achatinellidae. Since 1941, the research program as set forth by Dr. C. Montague Cooke, Jr. has called for the completion of the study of these groups through researches in anatomy. Basic conchological researches on the four groups above-named were wholly or in part completed by Pilsbry, Crampton, and Cooke. Pilsbry and Cooke have maintained that these researches cannot be considered as completed until the soft anatomy have been investigated and to this end Cooke has accumulated a vast store of soft parts for over 40 years in anticipation of it. We are now involved in the study of the genitalia, supplemented by studies of the teeth, central nervous system, and the pallial organs, primarily the kidney, of these four great groups, and a summary report of the research is in order.

Achatinellidae-Tornatellinidae. As a result of the large series of tornatellinid snails collected during the Mangarevan Expedition of 1934, it has been possible to make a rather thorough study of the anatomy of this group with the result that these two families have been revised and combined into one large group ACHATINELLIDAE. Within this group are 6 subfamilies, 11 tribes, 25 genera and 330 species. Of the 25 genera, 10 are new. The result of this research was obtained after six years of continuous study and will be published by 1955.

Partulidae. Pilsbry and Cooke made preliminary investigations on the soft anatomy of this wide-ranging land mollusk in 1934 and created three genera, namely, *Partula* (*s.s.*), *Samoana,* and *Eua.* Further investigations by us in 1947 showed that the species of Palau separate themselves into a fourth genus, namely, *Palaopartula* Pilsbry. A re-examination of the entire family by way of the soft anatomy is now in progress and a publication on its findings will be forthcoming in 1955 or 1956.

The conchological portion of the Partulidae, particularly that of the island of Raiatea, is still in the process of study by Henry E. Crampton of the American Museum.

Amastridae. The Amastridae has long been considered to be a family endemic to the Hawaiian Islands. However, in 1908 Pilsbry indicated that *Cochlicopa lubrica* (Müller) of the family Ferussacidae could not be separated anatomically from that of *Leptachatina* by any character of importance. Pursuing this clue, we began a systematic study of the Amastridae on anatomical grounds in 1946 though now it is in suspension. The study of this family will necessarily increase its scope to include the continental family Ferusssacidae and the result in its final form will undoubtedly be of great interest to the students of evolution and distribution.

Non-Endemic Families. Between 1938 and 1941 the Bishop Museum published a series of four parts of H. B. Baker's Zonitid Snails from Pacific Islands. Baker brought up to date the knowledge of this group principally through his research in anatomy, thus disposing of a group of land snails which is undoubtedly the most difficult one to treat on account of its simple shell structure.

During the same period W. J. Clench treated numerous species of the families Cyclophoridae, Pupinidae, and Synceridae, also published by Bishop Museum.

This leaves eight families still to be worked thoroughly of which the Endodontidae and Succineidae are the most extensive in point of numbers. Dr. Cooke has a partially completed manuscript of the Endodontidae; also a partially completed one on the Diplommatinidae. As Dr. Cooke stated on numerous occasions, in the Bishop Museum collection alone there is a sufficient material for five more generations of malacologists to do research upon.

TABULAR SUMMARY OF THE BISHOP MUSEUM COLLECTION OF LAND MOLLUSKS

SUBREGION	PER CENT COMPLETE	PER CENT PUBLISHED
Hawaii, leeward	75	0
Hawaii, main	70	50
Equatorial Islands	75	50
Juan Fernandez	10	90
Henderson	60	15
Mangareva	60	10
Tuamotu	60	40
Society	60	20
Samoa	50	15
Easter	5	5

SUBREGION	PER CENT COMPLETE	PER CENT PUBLISHED
Pitcairn	60	20
Rapa	60	15
Austral	70	30
Cook	60	10
Niue	40	5
Fiji	50	20
Santa Cruz	20	20
New Hebrides	25	75
Solomons	25	75
Bismarck	10	75
Admiralty	20	75
Bonin	50	90
Marianas	60	20
Palau	60	10
Carolines	60	20
Marshalls	10	10
Gilberts	5	5
Ellice	5	5
Phoenix	60	0

LAND MOLLUSCAN DISTRIBUTION IN THE SOUTHWEST PACIFIC

By A. W. B. Powell
Auckland Institute and Museum
Auckland, New Zealand

When I agreed to prepare a short paper on this topic I had not seen Mr. Y. Kondo's excellent summary of Terrestrial Malacological Research in the Central Pacific and Micronesia.

Actually this paper also covers the Southwest Pacific area upon which Mr. Turbott asked me to report.

I prefer therefore to make a small contribution to the discussion on Mr. Kondo's paper rather than to furnish an additional paper.

The references I should like to add refer to the New Zealand molluscan fauna but their inclusion in a summary of Southwest Pacific land snail research is not inappropriate since the genera concerned, *Placostylus* and *Delonagapia* (Powell, 1952), a new genus of the *Paryphantidae,* undoubtedly had their origin in the Melanesian area and must be considered comparatively recent migrants to New Zealand.

The genus *Delonagapia* is based upon a very small carnivorous snail formerly incorrectly assigned to the Hammulinid genus *Gerontia.*

I have published four papers on the genus *Placostylus* in New Zealand and these plus the one on *Delonagapia* are to be found in the *Records of the Auckland Institute and Museum* for the years 1947 to 1952 inclusive.

The *Placostylus* distributional studies deal with subspeciation in the Three Kings Islands and the northern mainland of New Zealand during the post Pleistocene to Recent period.

STATUS OF TAMARAW, *ANOA MINDORENSIS* (HEUDE)

By Canuto G. Manuel
National Museum, Manila, Philippines

Introduction

Tamaraw (Family Bovidae) is a dwarf type of buffalo endemic on the island of Mindoro, Philippines. Timaraw, a name apparently introduced by a certain writer, has been adopted in a number of publications. Among the Mangyans and other hill peoples of Southwestern Mindoro, the animal is called *anuang*.

Like many other forms of wildlife in the Philippines, the tamaraw is reported to be in a serious state of depletion. Its reported precarious situation, in addition to its controversial racial history and the fact that it is the largest indigenous animal in the Philippines, demands that a study of its present status be made with a view of formulating measures for its conservation.

It is the object of this paper to present the data obtained on the status of the tamaraw and to recommend measures for its conservation. The data presented in this paper were obtained from Occidental Mindoro in some parts of which small herds are still holding.

The difficulties of and dangers attendant to any actual close range observation of the tamaraw are largely responsible for gathering the information presented here from people who, at one time or another, have themselves actually known the habits of this animal.

Records show that a few live tamaraws have been kept in captivity, but the habits of the animal reported here are those of the wild state. A few known records of captive tamaraws may be worth mentioning. A live tamaraw was kept in the Mehan Gardens of the City of Manila. It died in the early twenties. Another tamaraw was kept at the Manila Aquarium of the Bureau of Science where it died sometime in 1933. In 1947, a live tamaraw was captured near Naujan, Oriental Mindoro. It was given as a gift to the late President Manuel A. Roxas of the Republic of the Philippines. This tamaraw, it was gathered, was later sent to the United States as a gift of the Filipino people to the San Francisco Zoo in California. The difficulties encountered in negotiations for its entry into the mainland of the United States resulted in its slaughter on board the ship, then anchored in San Francisco Bay. Mr. Enrique Zobel of Calatagan, Batangas Province, now has two female calves in captivity. According to him, the younger calf is about 9 months old while the other is a little over 2 years. Both came from the southcentral part of Occidental Mindoro.

The writer was in Occidental Mindoro in January, 1951, when the municipalities of Abra de Ilog, Mamburao and Sta. Cruz were visited. In June, 1953, the Municipality of San Jose was also visited. Unfortunately, no tamaraw was seen during these visits.

ACKNOWLEDGMENTS

The writer is indebted to the following who, in one way or another, have furnished valuable information that are used in this paper: Dr. Vicente de la Cruz and Mr. Benjamin Tordesillas, both of the Bureau of Forestry; Mr. Agapito Subido of the Bureau of Lands; Mr. Pedro de Mesa, a naturalist and for a long time a resident of Mindoro; and Mr. Enrique Zobel, a game enthusiast and who has 2 tamaraw calves in captivity.

THE ISLAND OF MINDORO

In a study of this nature, a knowledge of the environment under which the animal exists is essential. Many of the data presented in the following paragraphs were taken from Landicho's (1) Mindoro Yearbook.

The environment under which the tamaraw lives may be gleaned from the following brief description of the island of Mindoro where the species is confined.

Mindoro is located south of the island of Luzon. More specifically, it is located between 12° 15′ to 13° 32′ N. Lat. and 119° 58′ to 121° 55′ E. Long. It is roughly 150 kms. at its longest extent and 80 kms. at its widest. Its total area is slightly over 1,000,000 hectares or 10,000 sq. kms. Politically, this island is divided into Oriental (Eastern) and Occidental (Western) Mindoro Provinces. The eastern side where the northeast trade winds prevail from January to April is characterized by rainy and dry seasons. They are not, however, so pronounced as those prevailing in the western side from June to October. Occidental Mindoro, on the other hand, is exposed to the southwest monsoon characterized by heavy rains from June to October. Oriental Mindoro is relatively free from rains during these months. There are many rivers traversing the island; those on the eastern side are generally short and shallow while those on the western side are fewer but longer. The central ridge, from Cape Calavite to Buruncan Point, is covered with dense rain forests, which limit the climatic conditions obtaining on each particular side. The general contour of this portion of the island is rugged with high mountain peaks here and there. Mt. Halcon (2,580 meters) and Mt. Baco (2,487 meters) are the principal peaks in this section of the island. The tamaraw makes its abode in the forests of some of the mountains in the central ridge. The tall rushes of cogon (*Imperata cylindrica*) and talahib (*Saccharum spontaneum*) on either side, but principally on the western side, form the outer fringes and grazing areas of the tamaraw's range. These grasses are the characteristic vegetation on the western side of the island.

HABITS

Due perhaps to the ferocity of the tamaraw, the writer was not able to make a close-range study of this animal. The observations presented here are, therefore, pieced together from those gathered at various times by different people, some of whom are mentioned in this paper.

The tamaraw is nocturnal. It starts to move around late in the afternoon and retires in the morning. Taking advantage of this habit, tamaraw hunters search for it and for its fresh footprints at dawn and in late afternoon. Those who are familiar with the forests are of the opinion that the animal utilizes the deep, quiet portion of the dense forest as its retiring place. This habit obviously arises from its instinct to make use of its ears to full advantage for protective purposes. This information corroborates that of Worcester (5) who writes, "When the tamaraw retires, it lies down in the densest of the jungle growth facing back on its own trail." Its senses of hearing and smell are very well developed. These peculiarities of the tamaraw are taken advantage of by the hunters who, when watching for the animal, always place themselves against the direction from where the breeze and the tamaraw come. In this way, the tamaraw would not be able to use its ears and nose effectively.

During the months of June to October, when the southwest monsoon prevails, the rivers in Occidental Mindoro are swollen and the stream currents are rapid. During this period, the movements of the tamaraw are limited to the areas not traversed by rivers. This is also largely due to the fact that the tamaraw, unlike other members of the Family Bovidae, has not been known to take a dip in either a pool or stream. Thus, it avoids swollen rivers which are, at times, dangerous to cross. It was also pointed out that the tamaraw obviously dislikes rain. They were observed to dash for shelter as soon as it starts raining. In the dry months of January to May, however, the tamaraw wanders around feeding on tender shoots of cogon and talahib. Mr. Zobel observes that during these months, the tamaraw spends most of the time in the grazing areas. During the day the animal lies down to rest under very thick undergrowth which the natives call *gabon*. Occasionally, a small herd of two to five individuals may be seen early in the morning or late in the afternoon. This may be observed by patiently waiting at a strategic place along the tamaraw's trail to its feeding and drinking places. Worcester (5), however, claims that the tamaraw drinks at night. He (5) observed further, that the animal moves around in early morning to lick up ashes.

Food.—True to the peculiarities of the group, the tamaraw is herbivorous. In addition to cogon and talahib mentioned in the foregoing, the tamaraw is known to feed on kulapi (*Paspalum conjugatum*), luyaluyahan (*Panicum repens*), anabiong (*Trema orientalis*) and other plants, principally of the grass family.

Breeding.—Except when with a calf, a bull and a cow are generally seen together indicating that the species is monogamous. Sanchez (3) observes that the breeding season is from April to July. The same writer contends that the heat period lasts 24 hours and the cycle is every 3 weeks. The cow's oestral manifestations, according to Sanchez (3), are general restlessness, mounting other cows and a desire to lock horns with others.

Ferocity.—The fierceness of the tamaraw is known by all who have seen it or who have heard stories about it. This probably accounts for the great fear of the primitive hill people of Mindoro (Mangyans) for the tamaraw. It has been observed that a Mangyan cannot be made to approach a supposedly dead tamaraw no matter what happens unless he sees somebody else approach it first. In this connection, Worcester (5) claims that with rare exceptions, the tamaraw, when wounded, attacks fiercely, if it so much as catches sight of a human being. For reasons of safety, some hunters take their position on branches of large trees. This attitude, however, is no longer necessary, according to many hunters of late. With improved firearms, courage and alertness are all that are necessary. It is much better to watch them on their trails. In the forests, the tamaraw is very swift considering its size. Worcester (5) made a similar observation when he said that the tamaraw bores a hole through the jungle vegetation, coming on with the speed and recklessness of a rhinoceros. It is often remarked that when a tamaraw gets wounded, either the hunter kills the animal or the animal kills the hunter. This indicates the fierceness of the tamaraw as known to the people of Mindoro.

Wariness.—The tamaraw is fierce especially when wounded, but otherwise very wary. The least sign of danger which it notices through well-developed sense of hearing and small causes the tamaraw to run swiftly to safer places. When one member of the herd gets wounded, the others immediately turn back and swiftly run away. The natives observed that the tendency of the tamaraw when flushed is to run swiftly uphill through trails along very dangerous ridges. It is claimed by those who are familiar with the tamaraw that when in danger, either parent, but generally the mother, seizes the calf with her horns by passing them under the abdomen of the calf. The cow then raises her head and the calf slides behind her neck. With the forelegs of the calf hanging on one side and the hindlegs hanging on the other, the calf is securely saddled against the neck of the mother. And off she runs swiftly to a safer place.

Acts to Conserve Tamaraw

The first concrete evidence of the government's interest in the conservation of this rare animal was in 1920 when one of its known ranges, Mt. Calavite, was set aside as a game preserve. This preserve is situated in northwestern Occidental Mindoro. The preserve has an area of about 40,000 hectares. The Bureau of Forestry has also recommended Mt. Iglet in southcentral Occidental Mindoro as another preserve for the tamaraw. This, however, is still awaiting final congressional action. Meanwhile, reports indicate that the tamaraw moved further northeastward due to the fact that Mt. Iglet has lately been frequented by hunters. The designated would-be-preserve has an area of about 8,950 hectares.

A more specific measure to conserve the tamaraw is provided for in Commonwealth Act No. 73 of 1936, otherwise known as "AN ACT PROHIBITING THE KILLING, HUNTING, WOUNDING OR TAKING AWAY OF BUBALUS MINDORENSIS, COMMONLY KNOWN AS TAMARAW." Section 1 provides, "THE KILLING, HUNTING, WOUNDING, OR TAKING AWAY OF BUBALUS MINDORENSIS COMMONLY KNOWN AS TAMARAW, FOR ANY PURPOSE OTHER THAN THE PROTECTION OF PERSONS OR PROPERTY, OR FOR SCIENTIFIC ENDS DULY AUTHORIZED BY THE SECRETARY OF AGRICULTURE, IS HEREBY PROHIBITED." From the foregoing, it is evident that the law prohibits the taking of the tamaraw.

Causes of Depletion

The action of the government prohibiting the taking of the tamaraw was evidently the result of the significant reduction in its population caused undoubtedly by unscrupulous hunters. This step must have been taken after it was observed that the mere setting aside of a game preserve did not bring about the beneficial intentions of the government on the decimating species.

Poaching.—A careful perusal of the law cited above will reveal that it is vulnerable and can be violated with the flimsy excuse that the tamaraw was killed because it endangered the life of the hunter or that it was destructive to the property. The most important deterrent, however, is the fact that nobody enforces the law. A forest officer may be in a place far away from the tawaraw's range. There are no roads between his station and the range. It takes many days or weeks before he can reach the range. Moreover, his primary interest is centered around forest classification and violation of forestry laws, rules and regulations. The local police and the constabulary soldiers are deputized to apprehend violators of the game law, but generally, they are not interested in its enforcement. Under these conditions, aggravated by the fact that poachers generally live in the vicinity of the range or they are people with good connections, the law conserving the tamaraw is bound to fail in its intentions. It is interesting to note that obviously due to accessibility to centers of civilization, there are more tawaraws killed in Mt. Calavite and in Mt. Iglet than in other ranges combined. Mt. Calavite preserve can be reached within 10 hours from Manila by automobile, motor boat and a short hike. It is equally interesting to observe that people prominent in their respective communities and who can afford expensive hunting parties organize these parties to hunt the tamaraw for its meat, its hide, its horns or just for fun. There was only one occasion, as far as the writer can remember, when two tamaraws were killed for museum purposes. In 1933, former Governor-General Theodore Roosevelt, Jr. killed two animals for the Museum of Comparative Zoology, Harvard University.

A tamaraw hunting party generally consists of experienced guides, beaters, professional hunters and other skilled aides like cooks, utilities and others. It is well provided with both necessities and luxuries that can last for several days. Although the tamaraw is the object of the party, it also goes after other wildlife such as deer, wild pig, macaque, hornbill, pigeons and other game birds that are indiscriminately hunted. In expeditions of this nature, it may be expected that many types of firearms and ammunition that aggravate the destruction of wildlife are among the equipment and supplies of the party.

Changing environment.—It is conceded that man is the greatest enemy of wildlife. In Occidental Mindoro, kaiñgin or hill farming has been practiced since time immemorial. This consists of clearing and burning virgin forest to provide new areas for cultivation. After a few years, these are given up for other new areas. There are several lumber camps, whose activities are, directly or indirectly, detrimental to the tamaraw and other wildlife. In like manner, activities in mining camps and in newly created settlements tend to reduce wildlife in their vicinity of operation. In addition, the government's program of "land for the landless" signifies "no land" for wildlife. This policy, besides resulting in the reduction of the tamaraw's hereditary range, and limiting its natural environment, will necessarily have adverse effects on the animal's life as Mayr (2) points out that "once a species has become adapted to a set of environmental conditions, it will have a much reduced struggle for existence." When these areas are cleared for lumbering and mining camps and other developments, they will be exposed to extremes of weather conditions. Under this new set of environmental conditions, adult tamaraw will encounter difficulties of adjustment and the young will find it almost impossible to survive. The malaria control and the rodent control programs currently undertaken by the Foreign Operations Administration of the United States and the Philippine Council for the United States Aid doubtless also alter the conditions under which the tamaraw has been gradually adapted during its evolutionary processes. At the outset, all these programs designed to encourage the activities of man will have disastrous effects on wildlife.

Estimated Tamaraw Population

Considering the lack of interest of many people in tamaraw, it is of no wonder to expect difficulties that may be encountered in gathering data regarding the actual number of existing individuals. The difficulties become more manifest when visits made to places formerly occupied by the animal yielded discouraging results. For reasons they could not explain, the natives claim that the tamaraw disappeared in areas where they were formerly known to occur. These and the habits of the tamaraw described in a preceding paragraph should be taken into consideration when census taking of the animal fails. I should like, therefore, to believe the data presented in this paper as the best estimate available. They were supplied by field men of the Bureau of Forestry who are in Occidental Mindoro and who have observed the tamaraw in the course of their field activities for many years. Within the territorial limits of Occidental Mindoro, a total of approximately 244 tamaraws in about 19 herds is conservatively estimated to be holding their hereditary range. In a paper I prepared for the Seventh Pacific Science Congress, I indicated that it was doubted whether there were 1000 living tamaraws in Mindoro in 1949. That estimate was based on information supplied by tamaraw hunters.

It is unfortunate that no previous estimate has been made of the number of tamaraws. A definite basis cannot be established and, therefore, the status of the tamaraw population cannot be determined accurately. Some people claim that tamaraws were roaming the forests not far from their homes years ago but that they have since disappeared. Considering the wariness of the tamaraw, perhaps the experience of Prof. Steere as cited by Sclater (4), who obtained two males and one female within a short time while on a collecting trip in Mindoro in 1884, might give us an idea about the status of the tamaraw then. Likewise, Domingo Sanchez (3) secured two females and a male during a short trip in 1892. It should be noted that in those days, the firearms employed in hunting big animals were not as effective as they now are. With the modern, more powerful and more effective firearms, coupled with employment of experienced guides and better methods of hunting, bagging a tamaraw after a few days hunting is considered good luck for the hunter. These comparative data of bags are believed to be circumstantial proofs that the tamaraw population has reduced tremendously during the last half of the century, and unless measures to preserve the species are adopted, it is feared that extinction may take place in the not too distant future.

Recommendations for Conservation

It has been shown that the present situation of the tamaraw with only about 244 individuals holding in Occidental Mindoro is precarious. In the opinion of the writer, this condition is principally due to our indifference to conserve the species as evidenced by non-enforcement of conservation laws. Despite the law prohibiting hunting, killing, or even wounding the animal, it is still hunted within the preserve. It has also been pointed out that Act No. 73 is vulnerable and fraught with loopholes so that flimsy excuses, like the animal's endangering the life of the hunter or its inflicting damages on property, could be offered in case the hunter is apprehended. Surprisingly, no case of violation of Commonwealth Act No. 73 has been officially reported as far as the writer could gather. In order to eliminate the loopholes in the existing law, it is recommended that Commonwealth Act No. 73 be amended to strike out the clause on Section 1 dealing on exceptions. Section 1 of the law should then read as follows: "THE KILLING, HUNTING, WOUNDING OR TAKING AWAY OF ANOA MINDORENSIS, COMMONLY KNOWN AS TAMARAW, IS HEREBY PROHIBITED."

Rampant poaching, which is apparently due to legal defects of the law, neglect, disinterest or lack of facilities, should be checked immediately and remedial measures should be instituted. To avoid confusion among the enforcing agencies of the government, it is further recommended that only one agency be authorized to enforce the law.

The agency so chosen should be provided with adequate funds. In this way, responsibility with authority shall be concentrated in one office and the success or failure to preserve the dwindling stock of the tamaraw, can be determined more accurately.

There should be set aside, hand in hand with the development program of the government, a continuous range for game preserve along the central ridge extending from Mt. Calavite to the area beyond Mt. Iglet with sufficient grazing areas along both sides of the mountain range.

Summary

1. Tamaraw is a dwarf type of buffalo endemic on the island of Mindoro.
2. Tamaraw is reported to undergo a serious state of depletion. It is thus important that its status be determined so that conservation measures may be formulated.
3. Dangers attendant to a close range study of the tamaraw are largely responsible for gathering information on the habits of tamaraw presented here from people who are themselves familiar with the habits of this wild animal.
4. Tamaraw can be kept in captivity, some for a long time as shown by five cases in recent years.
5. Tamaraw is nocturnal. It retires in the depths of dense rain forests in certain areas along the central ridge of Mindoro. The areas of tall rushes along the forest borders principally along the western side are included in the grazing range of the tamaraw. During the dry season, the animal spends much of its time in the grazing areas. Thick underbush which the natives call *gabon* is used for shelter against rain. The food consists largely of grasses. Tamaraw, unlike other bovine animals, is not fond of dipping in water or of wallowing.
6. There is evidence to believe tamaraw is monogamous. It was observed that the breeding season of tamaraw is from April to July. Tamaraw is ferocious especially when wounded. Like other wild animals, it is wary. Its auditory and olfactory senses appear to be very well developed.
7. There is a game preserve in Mindoro intended primarily for tamaraw. Another preserve has been set aside and has, for sometime, been awaiting congressional action.
8. Tamaraw, which is protected by law, is being hunted within the preserve. Evidently the laws, rules and regulations to conserve tamaraw are not enforced.

9. Poaching is the most important factor in the destruction of the tamaraw.
10. Kaiñgin or hill farming, lumber and mining camps and opening of new settlements are indirectly causing destruction of the species. With the exploitation of the natural resources, the environmental conditions in the hereditary range of the tamaraw are altered, sometimes destroyed.
11. It is conservatively estimated that 244 tamaraws in 19 herds still exist. Due to lack of past records, the status of the tamaraw is deciphered through circumstantial proofs.
12. Measures to conserve the tamaraw include recommendation amending Commonwealth Act No. 73, to concentrate in one office of the enforcement of the tamaraw conservation laws, rules and regulations. A continuous game preserve from Mt. Calavite to an area beyond Mt. Iglet, which should include a strip along its western border for grazing, is also recommended.

LITERATURE CITED

1. LANDICHO, M. Z. The Mindoro Yearbook. (1952) 599 pp. Yearbook Publishers, Manila.
2. MAYR, E. Bird Conservation Problems in the South Pacific. Audubon Magazine, Sept.-Oct. (1945) p. 280.
3. SANCHEZ, D. La Ilustración Filipina. *2* (1892) no. 34, p. 268.
4. SCLATER, P. L. *Nature*. *38* (1888) p. 364.
5. WORCESTER, D. C. The Philippines, Past and Present. *2* (1914) pp. 824-827.

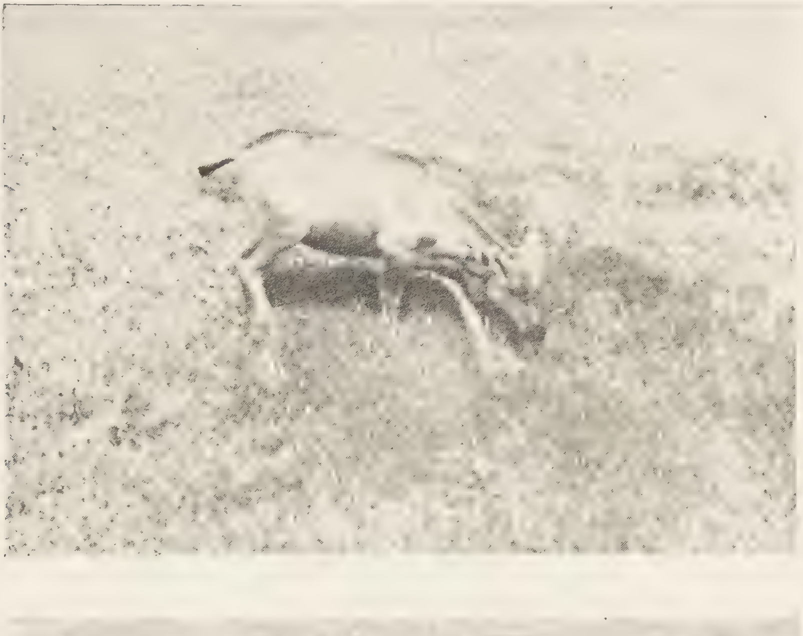


PLATE I

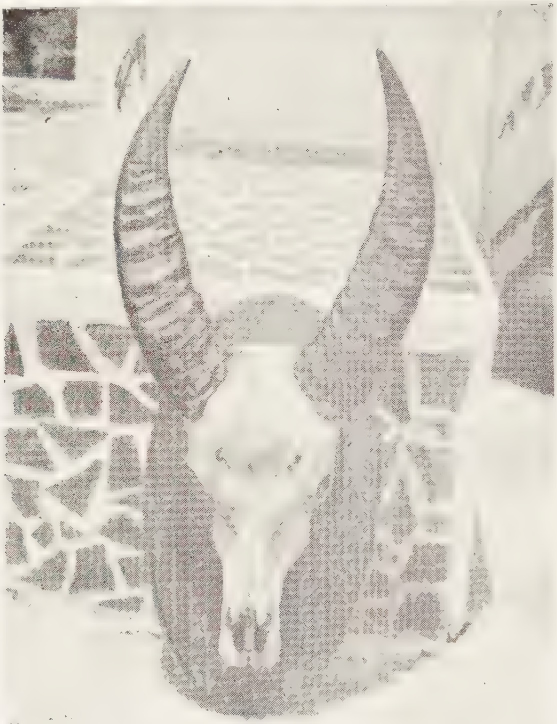


PLATE II

COLLECTION AND DISTRIBUTION OF BENEFICIAL INSECTS IN THE PACIFIC AREA AND SOUTHEAST ASIA

By T. R. Gardner
Bureau of Entomology and Plant Quarantine
Agricultural Research Administration
United States Department of Agriculture
Beltsville, Maryland, U.S.A.

Since the end of World War II, the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture has been actively engaged in the collection of parasites and predators in the Pacific Area and Southeast Asia for colonization against insect pests in the United States, Hawaii and Mexico, and in the distribution of the parasites and predators of various insect pests in the Pacific area. These include the natural enemies of the oriental fruit fly, *Dacus dorsalis* Hendl., citrus blackfly *Aleurocanthus woglumi* Ashby, spiny blackfly, *Aleurocanthus spiniferous* (Quaint.), pink bollworm, *Pectinophora gossypiella* (Saund.), European corn borer, *Pyrausta nubilalis* (Hbn.), tobacco budworm, *Heliothis* (*Chloridea*) *assulta* Gn., green peach aphid, *Myzus persicae* (Sulz.), and the coccinellid *Epilachna philippinensis* Dieke.

The oriental fruit fly was first observed in 1946 in Hawaii where it soon became a pest of major importance on fruit and vegetables. Recognizing the potentialities of this pest the Hawaiian Territorial Board of Agriculture sent a man to the Philippines in search of natural enemies of fruit flies in 1947. From July 1948 to the end of 1951 the U. S. Bureau of Entomology and Plant Quarantine, in cooperation with the Territorial Board of Agriculture and Forestry, the University of Hawaii Agricultural Experiment Station, the Pineapple Research Institute, the Hawaiian Sugar Planters' Association Experiment Station and the University of California Agricultural Experiment Station sent a number of entomologists to Africa, Brazil, India, Siam, Southeast China, Ceylon, North Borneo, Australia, New Zealand, New Caledonia, the Philippines and several other small Islands in the Pacific area to collect parasites of fruit flies and ship them to the Bureau's laboratory in Honolulu. During this period representatives of the various agencies sent about 600 shipments containing over 4 million fruit fly puparia representing over 60 species and varieties of fruit flies from about 110 different kinds of fruit. In addition, over 6 thousand adult parasites and predators of fruit flies were sent to Hawaii. These fruit fly puparia produced 200 thousand adult parasites of approximately 80 species including 45 species or color variants of the genus *Opius*. After thorough studies under quarantine conditions, about 25 species were liberated in the Hawaiian Islands, and of these, 11 apparently have become established.

During the past two years the Bureau has sent 13 shipments totaling about 35,000 adult fruit fly parasites, representing 5 species, from Hawaii to the United States for trial against the cherry fruit fly in California, Oregon and Washington. There is no indication at this time that any of these parasites have become established. A request from Bolivia, South America was fulfilled in September 1953 by sending one shipment containing about two thousand adults of 4 species of Opiine parasites for trial against fruit flies in that country. Another lot consisting of 152 *Opius oophilus* Fullaway, the egg parasite, was sent to Mexico in June.

In addition to these shipments 12 lots containing about 15 thousand adults of 11 species of parasites were sent from Honolulu by other agencies to Guam, Australia, Philippines, Italy and Greece from 1949 through 1953 for trial against various fruit flies in those countries. Also 22 thousand fruit fly pupae parasitized in the laboratory by *Opius oophilus* were sent to Fiji in 1951.

An infestation of the citrus blackfly, a serious pest of citrus, was discovered in Mexico in 1935 and since that time has gradually spread towards the United States border. In the summer of 1949, a Bureau representative was sent to India in search of natural enemies of this insect. As a result of investigations in India and Pakistan, 25 shipments consisting of 10 species of parasites and predators were sent to Mexico during late 1949 and early 1950. After quarantine rearing they were liberated in various parts of Mexico infested with the blackfly and 4 species, all Hymenoptera, became established. These are *Prospaltella clypealis* Silv., *Prospaltella smithi* Silv., *Prospaltella opulenta* Silv., and *Amitus hesperidum* Silv. Since then, the Bureau in cooperation with the Mexican National Committee for the Combat and Control of the Citrus Blackfly, has colonized these 4 parasites in most of the infested citrus areas throughout Mexico. Surveys indicate that this serious pest will be controlled by these parasites.

In 1952 a request was received from the entomologist on Guam for citrus blackfly parasites for trial against the spiny blackfly, *Aleurocanthus spiniferus* (Quaint.), a serious pest of citrus on that island. During the year 4 shipments containnig the parasites *P. clypealis, P. smithi, P. opulenta, Amitus hesperidum* and *Eretmocerus serius* Silv.

were sent to Guam from Mexico. *E. serius,* originally from Malaya, was introduced into Mexico from Panama in 1943 but is effective only in the moist, humid areas. A recent report from Guam states that *P. smithi, A. hesperidum* and *E. serius* are well established and have reduced infestations of *A. spiniferus* about 90 percent throughout the Island.

The pink bollworm, a serious pest of cotton in Southwestern United States, was discovered in Texas in 1917. Although parasites from several countries have been liberated in Texas to combat this pest, apparently none have become established. Since India probably is the native home of the pink bollworm, a representative of the Bureau was sent to India in 1952 in search of its parasites. Since arrival in that country he has sent 5 species of pink bollworm parasites collected in northern and central India to the Bureau's parasite receiving station at Moorestown, New Jersey. These include 4 thousand cocoons of *Bracon brevicornis* (Wesm.), a strain of *B. gelechiae* (Ashm.), approximately 42 thousand larvae parasitized by a species of *Apanteles,* and 9 thousand larvae parasitized by two species of *Chelonus.* During the past summer adults of these parasites were reared at Moorestown and shipped to Texas for colonization. It is too early to determine if any have become established.

Soon after the re-occupation of Guam after World War II, it was observed that corn on the Island was being severely damaged by the European corn borer. In order to combat this situation a request was received for parasites of the corn borer which had become established in the United States from imported material. As a result, 32 thousand borers were collected in the field and shipped to Guam early in 1952. From these borers, a total of 511 *Lydella stabulans grisescens* R.D., 3,105 *Macrocentrus gifuensis* Ashm., 142 *Horogenes punctorius* (Roman) and 319 *Chelonus annulipes* Wesm. were reared. Adults of all species were released at nine colony sites. The tachinid *L. grisescens* was reared from borers collected near the release sites indicating establishment, but no recoveries have ever been made of the three hymenopterous parasites. A further request for corn borer parasites was received from Guam this year and arrangements have been made to collect material this fall and ship it this winter.

A request for parasites of the European corn borer was also received from the Bureau of Plant Industry in the Philippines where it is a serious pest of corn. Ten thousand borers were collected this fall in the eastern part of the United States and brought to Manila for parasite rearing and colonization.

This year a request was received from the Bureau of Plant Industry in Manila for parasites of the so-called tobacco budworm, *Heliothis assulta,* a pest of tobacco in the Philippines. In June and July, *Campopletis perdistinctus* (*Sagaritis provancheri* D.T.), a parasite of *Heliothis virescens* (F.) on tobacco was collected in North Carolina and two shipments totaling 317 adults were sent by air to Manila in July. In August, 125 *Cardiochiles nigriceps* Vier. adults, another parasite of *H. virescens* were collected in North Carolina, and sent to Manila by air. These shipments arrived at their destination in very poor condition, due probably to abnormal temperatures en route. Of the latter species only two females were alive on arrival. These parasitized *assulta* larvae as soon as they were placed with them. Another lot of field collected, overwintering *H. virescens* pupae parasitized by *Campopletis* and *Cardiochiles* was brought to Manila and turned over to the Bureau of Plant Industry for further laboratory rearing and colonization against this tobacco insect.

The green peach aphid is a pest of tobacco in the Philippine Islands as it is in the United States. Adults of the ladybird, *Hippodamia convergens* Guer., which is known to feed on this aphid, were collected in California recently and brought by me to Manila for colonization in aphid-infested tobacco fields.

The coccinellid, *Epilachna philippinensis,* is a serious pest of certain truck crops on Guam, especially tomatoes and eggplants. In 1950 a request was received from Guam for *Paradexodes epilachnae* Ald., a common tachinid parasite of the Mexican bean beetle, *Epilachna varivestis* Muls. in Mexico. In the fall of the same year a representative of the Bureau stationed in Mexico sent two shipments totaling 9,960 *P. epilachnae* puparia to Guam via Hawaii for trial against this coccinellid. Apparently this species never became established.

In 1952 a second request was received from the Entomologist in Guam for additional puparia of this parasite. In October two shipments totaling 3,574 parasite puparia obtained from field-collected host larvae were sent from Mexico. Only 422 flies emerged from this material, due possibly to a high rate of hyperparasitization. No report has been received as to whether this parasite has become established in the Island.

No doubt there are many other parasites and predators in Southeast Asia and the Pacific Area that could be introduced into North and South America as well as exchanged between countries of Southeast Asia and the islands in the Pacific and utilized in the control of insect pests.

THE DISTRIBUTION OF TERRESTRIAL REPTILES IN THE ISLANDS OF THE PACIFIC BASIN

By Walter C. Brown
Natural History Museum
Stanford University, California, U.S.A.

1. Introduction

Our increased knowledge of the distribution and relationships of the terrestrial reptiles that inhabit the islands of the central Pacific does not greatly affect the overall pattern discussed by Mertens (1934, pp. 36–41). This is essentially a radial pattern from a center or centers in the Indo-Australian region (also Darlington, 1948, p. 119); but some details of the pattern are, I believe, better understood at this time.

The purpose of this paper is to consider the detailed distributional patterns and probable past history of this element of the Polynesian fauna in the light of our present knowledge.

The Polynesian Subregion extends from New Caledonia to the Tuamoto and Marquesas Islands along the southern border and from the Palaus and Marianas to the Hawaiian Islands along its northern border, but does not include the Bismarck and Solomon archipelagoes. The latter possess a much richer Papuan fauna and, although the Solomons exhibit a longer isolation with nineteen of fifty-one species endemic, both archipelagoes form a part of the Papuan Subregion.

The Polynesian Subregion lies almost wholly within the tropics which afford the most favorable conditions for an abundant and continually active reptilian fauna. Baker (1947, p. 246) reports that in New Hebrides *Emoia cyanura* and *Emoia werneri* (*Emoia callistica werneri*) are in breeding condition throughout the year with the possible exception of *Emoia callistica* in May. Both species reach a peak in November-December and their lowest point in May-June. The abundance of individuals observed on many of the islands is probably due in part, however, to the fact that the lizard populations are near maximum density having few or no enemies (Brown and Marshall, 1953).

The size of the island that is necessary for the successful maintenance of a population once it has arrived probably differs greatly for different species; but very small, low islands may be successfully occupied by some species (Mertens, 1934, p. 4 and Brown and Marshall, 1953). Also the size and nature of the island probably determine the number of species, occupying in part or entirely any given environmental niche, which can successfully coexist. *Emoia boettgeri* and *Emoia arnoensis,* for example, do not occur on the same islet in Arno Atoll (see Brown and Marshall, 1953), but these two species are both known to occur on Kusaie Island, a large, high island in the eastern Carolines.

The niche inhabited by a given species also greatly affects its opportunities for dispersal from island to island. In general the most widespread species live in or near man's habitations or in beach or strand habitats. For example *Emoia atrocostata,* which lives along the beach areas, is widespread and is probably very favorably situated for chance dispersal by flotation methods.

2. Composition of the Fauna and Natural Subdivisions of the Subregion

At the present time twenty-six genera and seventy-four species of terrestrial reptiles are generally recognized. These belong to the following families: Geckonidae with ten genera and twenty-one species, Agamidae with one genus and one species, Iguanidae with two genera and two species, Varanidae with one genus and two species, Scincidae with eight genera and thirty-eight species, Typhlopidae with one genus and four species, Boidae with one genus and three species, Colubridae with one genus and two species, Elapidae with one genus and one species, and Trionchydae with one genus and one species.

Thirteen species are of little or no value in zoogeographic studies. They are either known to have been recently introduced or because of their habits or wide distribution remain suspect of a dispersal closely associated with man's economy. *Trionyx sinensis, Anolis carolinensis* and *Typhlops braminus* are known to be recent introductions into the Hawaiian Islands (Slevin, 1930, p. 158, Shaw and Breese, 1951, p. 68 and Oliver and Shaw, 1953, p. 69). The latter also occurs in the Marianas Islands but its introduction is probably unknown.

Four, *Gehyra oceanica, Gymnodactylus pelagicus, Ablepharus boutoni* and *Lygosoma (Leiolopisma) noctua,* are Papuan species with a very wide distribution in the Pacific islands. Five, *Gehyra mutilata, Hemidactylus garnoti, Hemidactylus frenatus, Hemiphyllodactylus typus* and *Lepidodactylus lugubris* range from southern or southeastern Asia through the Indo-Australian Archipelago and the Philippines and have general or scattered distributions in the Polynesian region. More complete collecting will probably show that all nine species are widely distributed. *Lygosoma (Leiolopisma) metallicum* is an Australian species with records showing a spotty distribution in the Pacific islands. Five species of Emoia with rather wide distribution in the western part or throughout Polynesia are not included at this point but will be considered separately.

When one considered the subdivision of the Polynesian Subregion on the basis of differences and similarities in the reptilian faunas, excluding the widespread species previously listed, the basic subdivisions are in reasonably close agreement with those of Mayr (1940a) based on the avian faunas even though the means of dispersal for the reptiles probably differ greatly. The greatest discrepancy is the inclusion of the Hawaiian Islands in the eastern Polynesian subdivision. Southern Melanesia, though retained, is not as clearly defined on the basis of its reptilian fauna as it was on the basis of its birds. New Caledonia is even more unique and is tied to the rest of the subdivision by virtue of its contribution to the fauna of the Loyalty Islands. Each of the subdivisions will be dealt with separately as to the composition and relationships of its fauna.

Micronesia—Eighteen genera (none endemic) with thirty-one species are known. Eight species are included in the widespread or recently introduced species. Of the remaining twenty-three species, seven (30.4 per cent) are endemic; twelve (52.2 per cent) are not known from any other subdivision of Polynesia. Seven, including three endemic species, have their closest affinities with the Philippine fauna; sixteen, including nine species of *Emoia*, four of which are endemic, have Papuan affinities. These probably entered by way of the Bismarcks except *Emoia cyanura*, which apparently centered by way of Eastern or Central Polynesia, since it was known only from the Marshall and eastern Caroline Islands until a single specimen (U.S.N.M.) was recently recorded from Guam. There is a gradual reduction in the number of genera and species from west to east in Micronesia. *Typhlops, Enygrus, Dendrolaphis, Mabuya, Lygosoma* (*Sphenomorphus*), *Varanus* and *Gonyocephalus* occur only in the most western part of Micronesia and include only one endemic species, *Typhlops acuticauda* from the Palau Islands. Four of the seven species with Philippine affinities are known only from the Palaus.

TABLE I

Number of Genera and Species Known from the Principal Island Groups of Micronesia

	Palaus	Carolines	Marianas	Marshalls
Genera	14	11	6	8
Species	19	19	8	11
Endemic[1]	3		1	

---

[1] Of the seven species endemic to Micronesia three are known from both the Caroline and Marshall Islands.

Southern Melanesia—Sixteen genera (three endemic) with forty-eight species are known. Nine species are widespread or apparently recently introduced. Of the remaining thirty-nine species, twenty-six (68.4 per cent) are endemic; twenty-seven (69.2 per cent) art not known from other subdivisions. Eighteen, including five endemic species, have their closest affinities with the Papuan fauna (eight with the endemic species belong to the genus *Emoia*.); twenty-one endemic species, all but one limited to New Caledonia and the Loyalty Islands, are presumably of Australian affinities. *Emoia samoensis* and *Emoia cyanura* are species of Papuan origin, which probably underwent their evolution in Central Polynesia or, in the instance of the latter, Northern Melanesia. *Emoia samoensis* has succeeded in reaching the Solomons and *Emoia cyanura* is widespread throughout Northern Melanesia but has not reached or succeeded in becoming established in New Guinea or western Micronesia.

The fauna of the Santa Cruz and Banks Islands is a very impoverished Papuan one. The New Hebrides have a richer Papuan fauna, including two endemic species, and one species which has entered from New Caledonia. The Loyalty Islands, which are located close to New Caledonia, oddly have a predominately Papuan fauna. Seven of sixteen recorded species are widespread. Six of these have entered by way of Papua and five have reached New Caledonia. Four other species of Papuan relationship are not known from New Caledonia. Four of presumed Australian affinities and one which is Papuan are limited to the Loyalties and New Caledonia. New Caledonia has a highly endemic fauna probably of Australian origin. Only eight of twenty-nine species, five widespread, one endemic and one known otherwise only from the Loyalty Islands, and *Emoia callistica* (an apparently recently introduced species) are definitely Papuan.

TABLE II
NUMBER OF GENERA AND SPECIES KNOWN FROM THE PRINCIPAL ISLAND GROUPS OF SOUTHERN MELANESIA

	SANTA CRUZ	BANKS	NEW HEBRIDES	LOYALTIES	NEW CALEDONIA
Genera	9	6	8	12	11
Endemic					2 [a]
Species	13	8	18	16	29
Endemic			2	1	18 [b]

[a] One additional genus, Bavayia, is known otherwise only from the Loyalties.
[b] Four additional species are known otherwise only from the Loyalties.

Central Polynesia—Fourteen genera (two endemic) with twenty-one species are known. Seven species are included in the widespread species.

Of the remaining fourteen species, six (42.8 per cent) are endemic; seven (50 per cent) do not occur in any other subdivision. Two of the endemic species are of unknown affinities and twelve including the other endemics are Papuan. Six of the Papuan species including two endemics belong to the genus *Emoia*. The Fiji Islands have a richer fauna than other, more eastern island groups.

TABLE III
Number of Genera and Species Known from the Principal Island Groups of Central Polynesia

	Fiji Ids.	Samoa Ids.	Tonga Ids.	Union Ids.
Genera	11	7	9	5
Endemic	1[a]			
Species	16	11	12	5
Endemic	2[a]	1	1	

[a] *Brachylophus fasciatus* is a third species which is known from the Tonga as well as Fiji Islands.

Eastern Polynesia—Eleven genera and thirteen species are recorded from Eastern Polynesia. As previously noted, three genera, each with one species, and *Lygosoma* (*Leiolopisma*) *metallicum* are relatively recent introductions to the Hawaiian Islands. *Emoia cyanogaster* has been erroneously recorded for the Cook Islands (Burt and Burt, 1932, p. 520). The specimens (A.M.N.H. 29246–47)* are examples of *Emoia cyanura*. The remaining nine species representing eight genera belong to the group which is widespread in the Pacific Islands. Seven species of this group constitute the fauna of the Hawaiian Islands prior to known, recent introductions.

3. Summary and Some General Considerations

The terrestrial reptiles of the Polynesian Subregion are largely Papuan (50.7 per cent) but includes four other elements. Of the seventy-five known species, one recently introduced is American, seven among the widespread or recently introduced are Indo-Australian or Asiatic species, seven are derived from the Philippine fauna and twenty-two, including twenty endemic to New Caledonia and the Loyalty Islands, are presumably largely Australian. If New Caledonia and the Loyalties are not included in this Subregion, the percentage of Papuan species becomes 69.1 per cent. The Australian influence is almost wholly limited to New Caledonia and the Loyalty Islands and the Philippine influence to the Palau and western Caroline Islands.

---

* A.M.N.H. = American Museum of Natural History, New York.

Of the thirteen species earlier mentioned which are of little use in zoogeographic studies, excluding two recently introduced into the Hawaiian Islands and a third into both the Hawaiians and Marianas,[1] ten occur so generally throughout the Pacific area or show such scattered distribution that it is probable that their dispersal has been closely associated with man's economy. When these thirteen species are excluded, no one of the subdivisions recognized has more than fifty per cent of its reptilian fauna in common with any other subdivision. Five species of *Emoia* (*atrocostata, callistica, cyanogaster, cyanura* and *mivarti*) are suspect of being at least in part aided by man in their dispersal.

Of the remaining sixty-one species, thirty-nine (63.9 per cent) are endemic.[2] Twelve of these belong to endemic genera, three being geckonid genera with ten species limited to New Caledonia with the exceptions of one species which also occurs in the Loyalty Islands; one iguanid genus with one species known from the Fiji and Tonga Islands and an elaphid genus with one species known only from the Fijis. These represent the oldest element of the reptilian fauna, a select fauna; and these islands are undoubtedly very old islands that have served as secondary centers of dispersal. Similar reversed dispersal patterns are also evident in the avian fauna (Mayr, 1940b, p. 211). Whether or not this fauna reached these islands by way of continental connections cannot be positively stated but seems most unlikely in view of the probable age of such hypothetical connections. This is further supported by the evidence from the distribution of fresh-water fishes and amphibians (see Myers, 1951, and *Proc. 7th Pac. Sci. Congress,* vol. IV, 1953). However, the fact that they have not to any extent succeeded in crossing the present sea barriers suggests that they probably reached the islands at a time when the sea barriers were not as extensive as they are today.

The other islands of Central Polynesia and Southern Melanesia as well as Micronesia and Eastern Polynesia would appear to have received their present reptilian faunas at a more recent time since they possess no endemic genera. However, the evidence suggests that some of the high and more stable islands in Micronesia, as Kusaie and Ponape in the eastern Carolines, may similarly have served, though to a lesser extent, as reservoirs and secondary centers of dispersal.

Of the non-endemic genera, the Papuan, scincoid genus *Emoia* has apparently undergone the greatest speciation in the islands of the Polynesian Subregion as a whole, being represented as previously noted, by four endemic to Micronesia and four endemic to Southern Melanesia and Central Polynesia. This suggests that this genus, along with *Riopa* in Southern Melanesia and Central Polynesia and *Perochirus* in Micronesia, represents the second oldest element in the fauna of the Polynesian islands, or we must postulate a much more rapid evolution. It is largely Papuan with the smaller Philippine element in Micronesia.

---

[1] Dr. J. L. Gressitt (personal communication) states that *Anolis* is apparently established on Guam Island.

[2] This includes five species of the genus *Emoia*, five of which have been known for some time, and three recently described (Brown and Marshall, 1953 and Brown, 1954).

Of the thirty-six non-endemic species, thirteen are recently introduced or widespread; four are Philippine, limited to western Micronesia, and the rest are Papuan only a few of which are even sub-specifically differentiated. The ophidian, varanid and agamid genera in the Papuan and Philippine Subregions have reached only the western edge of Polynesia, except for *Enygrus* (Boidae) with two species as far east as the Fiji and Samoa Islands and as far south as New Hebrides. These thirty-six species, primarily Papuan but with a small Philippine element in western Micronesia, are the third and most recent reptilian fauna to enter Polynesia and their dispersal is also probably in part, but not wholly, associated with man's movements. Knowledge of the ecological limitations of the various species and their possible effect on their distribution and successful colonization of any given island is greatly needed.

LITERATURE CITED

BAKER, J. R. 1947. The seasons in a tropical rain-forest. Part 6. Lizards (*Emoia*). *Journ. Linn. Soc. London*, 41: pp. 243-247.

BROWN, WALTER C. and JOE T. MARSHALL, JR. 1953. New scincoid lizards from the Marshall Islands, with notes on their distribution. *Copeia*, 1953, No. 4, pp. 201-207.

BURT, CHARLES E. and MAY D. BURT. 1932. Herpetological results of the Whitney south sea expedition. VI. *Bull. Amer. Mus. Nat. Hist.*, 63, pp. 461-597, 38 figs.

DARLINGTON, P. J. 1948. The geographical distribution of cold-blooded vertebrates. *Quart. Rev. Biol.*, 23, pp. 1-26, 105-123.

MAYR, ERNST. 1941a. Borders and subdivisions of the Polynesian region as based on our knowledge of the distribution of birds. *Proc. 6th Pac. Sci. Congress*, 4, pp. 191-195.

MERTENS, ROBERT. 1934. *Die Insel-Reptilien, ihre Ausbreitung, Variation und Artbildung*. Zoologica, Stuttgart, 32, pp. 1-209, pls. 1-6.

MYERS, GEORGE S. 1951. Fresh-water fishes and East Indian zoogeography. *Stanford Ichthyological Bull.*, 4, No. 1, pp. 11-21.

————. 1953. Ability of amphibians to cross sea barriers, with especial reference to Pacific zoogeography. *Proc. 7th Pac. Sci. Congress*, 4, pp. 19-26.

OLIVER, JAMES A. and CHARLES E. SHAW. 1953. The amphibians and reptiles of the Hawaiian Islands. *Zoologica*, New York, 38, pp. 65-95.

SHAW, CHARLES E. and PAUL BREESE. 1951. An addition to the herpetofauna of Hawaii. *Herpetologica*, 7, p. 68.

SLEVIN, JOSEPH R. 1930. A note on the discovery of the genus *Typhlops* in the Hawaiian Islands. *Copeia*, **1930**, No. 4, p. 158.

TABLE IV

Distribution of Terrestrial Reptiles in the Pacific Islands

Family	Species	Micronesia	Southern Melanesia	Central Polynesia	Eastern Polynesia
	Lygosoma (Leiolopisma) austrocalidonicum		x		
	Lygosoma (Leiolopisma) euryotis		x		
	Lygosoma (Leiolopisma) gracile		x		
	Lygosoma (Leiolopisma) mariae		x		
	Lygosoma (Leiolopisma) metallicum		x		x
	Lygosoma (Leiolopisma) nigromarginata		x		
	Lygosoma (Leiolopisma) noctua	x	x	x	x
	Lygosoma (Leiolopisma) novae-caledoniae		x		
	Lygosoma (Leiolopisma) slevini		x		
	Lygosoma (Leiolopisma) steindachneri		x		
	Lygosoma (Leiolopisma) tricolor		x		
	Lygosoma (Leiolopisma) variabile		x		
	Lygosoma (Sphenomorphus) deplanchi		x		
	Lygosoma (Sphenomorphus) sp. ?	x			
	Mabuya multicarinata	x			
	Mabuya multifasciata	x			
	Riopa albofasciolata	x	x		
	Riopa baucourti		x		
	Riopa garnieri		x		
	Riopa microlepis			x	
Typhlopidae	*Typhlops acuticauda*	x			
	Typhlops aluensis			x	
	Typhlops braminus	x			x
	Typhlops willeri		x		
Boidae	*Enygrus australis*		x	x	
	Enygrus bibroni		x	x	
	Enygrus carinatus	x	x		
Colubridae	*Dendrelaphis calligaster*		x		
	Dendrelaphis lineolatus	x			
Elapidae	*Ogmodon vitianus*				x

TABLE IV (Continued)

FAMILY	SPECIES	MICRONESIA	SOUTHERN MELANESIA	CENTRAL POLYNESIA	EASTERN POLYNESIA
Trionchydae	*Trionyx sinensis*		x		x
Geckonidae	*Bavayia cyclura*		x		
	Bavayia sauvagi		x		
	Eurydactylus symmetricus		x		
	Eurydactylus vieillardi		x		
	Gecko vittatus	x	x		
	Gehyra brevipalmata	x			
	Gehyra mutilata	x	x		x
	Gehyra oceania	x	x	x	x
	Gymnodactylus pelagicus	x	x	x	
	Hemidactylus frenatus	x			
	Hemidactylus garnoti		x		x
	Hemiphyllodactylus typus		x	x	x
	Lepidodactylus lugubris	x	x	x	x
	Lepidodactylus manni			x	
	Perochirus articulatus	x			
	Rachodactylus ariculatus		x		
	Rachodactylus chahoua		x		
	Rachodactylus ciliatus		x		
	Rachodactylus leachianus		x		
	Rachodactylus sarasinorum		x		
	Rachodactylus trachyrhynchus		x		
Agamidae	*Gonyocephalus godeffroyi*	x		x	
Iguanidae	*Brachylophus fasciatus*			x	
	Anolis carolinensis	x			x
Varanidae	*Varanus indicus*	x			
	Varanus salvator	x			
Scincidae	*Ablepharus boutoni*	x	x	x	x
	Dasia smaragdina	x	x		
	Emoia adspersa			x	
	Emoia arnoensis	x			
Scincidae	*Emoia atrocostata*	x	x		
	Emoia boettgeri	x			
	Emoia callistica	x	x		
	Emoia cyanogaster	x	x	x	
	Emoia cyanura	x	x	x	x
	Emoia mivarti	x			
	Emoia nigra		x	x	
	Emoia murphyi			x	
	Emoia nigromarginata		x		
	Emoia samoensis		x	x	
	Emoia speiseri		x		
	Emoia n. sp.	x			
	Emoia n. sp.	x			

APPENDIX

The following list is not intended as a complete bibliography on the herpetofauna of the islands of the Pacific Basin. The early references; the principal, regional and revisional studies and selected short papers concerned with the reptilian fauna of the Polynesian Region are included. It is intended that the list may serve as a basic reference list and guide to the literature.

ADAMSON, A. M. 1939. Review of the fauna of the Marquesas Islands and discussion of its origin. Reptilia. *Pacif. Entom. Survey Honolulu Pub.*, **10**, 1939, pp. 63-64.

ANGEL, F. 1935. Liste des reptiles recoltes par la Mission Aubert de la Rue aux Nouvelles Hebrides ou dans les iles voisines. *Bull. Mus. Hist. nat. Paris* (2) 7, pp. 54-56.

ATOKA, K. 1950. Metamorphosis of the "non-aquatic frog" of the Palau Islands, western Carolines. *Pac. Sci.*, **4**, pp. 202-227.

BAKER, J. R. 1928. The non-marine vertebrate fauna of the New Hebrides. *Ann. Mag. Nat. Hist.*, (10) **2**, pp. 294-302.

——— 1947. The seasons in a tropical rain-forest. Part 6. Lizards (*Emoia*). *J. Linn. Soc. London*, **41**, pp. 243-247.

BARBOUR, THOMAS. 1912. A contribution to the zoogeography of the East Indian Islands. *Mem. Mus. Comp. Zool.*, **44**, pp. 1-203, pls. i-viii.

——— 1923. The frogs of the Fiji Islands. *Proc. Acad. Nat. Sci. Philadelphia*, **75**, pp. 111-115.

BOULENGER, G. A. 1885a. Catalogue of the lizards in the British Museum, (ed. 2, London), **1**, i-xii + 436 pp., pls. i-xxxii.

——— 1885b. Catalogue of the lizards in the British Museum. (ed. 2, London), **2**, i-xiii + 497 pp., pls. i-xxiv.

——— 1886. On the reptiles and batrachians of the Solomon Islands. *Trans. Zool. Soc. London*, **12**, pp. 35-62, pls. vii-xiii.

——— 1887. Catalogue of the lizards in the British Museum. (ed. 2, London), **3**, i-xii + 575 pp., pls. i-xl.

——— 1893. Catalogue of the snakes in the British Museum. (ed. 2, London), **1**, pp. i-xii + 488 pp., pls. i-xxvii.

——— 1894. Catalogue of the snakes in the British Museum. (ed. 2, London), **2**, i-xi + 382 pp., pls. i-xx.

——— 1896. Catalogue of the snakes in the British Museum. (ed. 2, London), **3**, i-xiv + 727 pp., pls. i-xxv.

BRONGERSMA, L. D. 1932. Some note on the genus *Hemiphyllodactylus* Bleeker. *Zool. Med. Leiden*, **14**, pp. 211-223.

BROWN, W. C. 1952. The amphibians of the Solomon Islands. *Bull. Mus. Comp. Zool.*, **107**, pp. 1-64, pls. i-viii.

——— 1954. A revision of the lizards of the genus *Emoia*, with observations on their distribution and evolution, (in press), Stanford University.

BROWN, W. C. and J. T. MARSHALL. 1953. New scincoid lizards from the Marshall Islands, with notes on their distribution. *Copeia*, No. 4, pp. 201-207.

BROWN, W. C. and V. M. TURNER. 1949. Rediscovery of the genus *Pseudogekko* with description of a new species from the Solomon Islands. *Gt. Basin Nat.*, 9, pp. 41-45.

BURT, C. E. and M. D. BURT. 1932. Herpetological results of the Whitney south sea expedition. VI. Pacific island amphibians and reptiles in the collection of the American Museum of Natural History. *Bull. Amer. Mus. Nat. Hist.*, New York, **63**, pp. 461-597.

DE ROOIJ, NELLY. 1915. The reptiles of the Indo-Australian archipelago. I. Lacertilla, Chelonia, Emydosauria, Leiden, i-xiv + 384 pp.

———— 1917. The reptiles of the Indo-Australian archipelago. II. Ophidia. Leiden, i-xiv + 334 pp.

DUMÉRIL, A. M. C. and G. BIBRON. 1839. Erpétologie Général, 5, pp. 1-857, pls. xlix-lviii.

DUMÉRIL, A. M. C. and AUG. DUMÉRIL. 1851. Catalogue méthodique de la collection du Muséum d'Histoire Naturelle de Paris. Paris, i-iv + 224 pp.

FISCHER, J. G. 1886. Herpetologische Notizen. *Abh. Naturw. Ver. Hamburg*, 9, pp. 51-67, pls. i-ii.

FITZINGER, LEOPOLDO. 1843. Systema reptilium, Vienna, Fasc. 1, i-ix + 106 pp.

GARMAN, SAMUEL. 1908. The reptiles of Easter Island. *Bull. Mus. Comp. Zool.*, 52, pp. 1-14.

GIRARD, CHARLES. 1858. United States exploring expedition during the years 1838-1842 under the command of Charles Wilkes, U.S.N., **20**, Herpetology, i-xvii + 496 pp. and atlas, pp. 1-10, pls. i-xxiii.

HEDIGER, HEINE. 1933. Über die von Herrn Dr. A. Buhler auf der Admiralitats-gruppe und einigen benachbarten Inseln gesammelten Reptilien

HEDIGER, HEINE. 1934. Beitrag zur Herpetologie und Zoogeographie Neu Britanniens. *Zool. Jahrb. Syst. Jena*, **65**, pp. 441-582.

———— 1937. Seltsame Reptilien und Amphibien der Solomon-Inseln. *Natur und Volk*, 67, pp. 590-595.

JACQUINOT, H. and A. GUICHENOT. 1853. Reptiles in Hombron and Guichenot, voyage au pole sud et dans l'oceanie sur les corvettes l'Astrolabe et Zelee. Paris, Zoologie, **3**, pp. 1-28.

KINGHORN, J. R. 1928. Herpetology of the Solomon Islands. *Rec. Austral. Mus. Sydney*, **16**, pp. 123-178, pls. xiii-xv.

————1937. A new species of Scink from the Solomon Islands. *Rec. Austral. Mus. Sydney*, **20**, pp. 1-2, pl. i.

KISHIDA, K. 1929. A new monitor from the island of Saipan, south sea islands. *Lansania Tokyo*, **1**, pp. 13-16.

LESSON, R. P. 1830. Zoologie, in M. L. I. Duperry, voyage autour du monde . . . sur la corvette de sa Majesti, La Coquille, pendant les années 1822, 1823, 1824, et 1825. Paris, i-iv + 743 pages and atlas of 157 pls.

LOVERIDGE, ARTHUR. 1948. New Guinean reptiles and amphibians in the Museum of Comparative Zoology and United States National Museum. *Bull. Mus. Comp. Zool.*, **101**, pp. 205-430.

———— 1941. An undescribed skink (*Lygosoma*) from New Caledonia. *Proc. Biol. Soc., Wash.*, 54, pp. 175-178.

MCGREGOR, R. C. 1904. Notes on Hawaiian reptiles from the island of Maui. *Proc. U.S. Nat. Mus.*, 28, pp. 115-118.

MERTENS, ROBERT. 1929. Die Rassen des Smaragdskinkes, *Dasia smaragdinum* Lesson. *Zool. Anz.*, **84**, pp. 209-220.

——— 1931. *Ablepharus boutonii* (Desjardin) und seine geographische Variation. *Zool. Jahrb. Syst., Jena*, **61**, pp. 63-210, pls.

——— 1934. Die Insel—Reptilien, ihre Ausbreitung, Variation und Artbildung. *Zoologica, Stuttgart*, **32**, pp. 1-209, pls. 1-6.

——— 1942. Die Familie der Warane (Varanidae). 1, 2 & 3. *Abh. senckenberg. naturf. Ges.*, Nos. 463-465, pp. 1-391.

OLIVER, J. A. and C. E. SHAW. 1953. The amphibians and reptiles of the Hawaiian Islands. *Zoologica, New York*, **38**, pp. 65-95.

PARKER, H. W. 1925. Notes on lizards from the south Pacific islands. *Ann. Mag. Nat. Hist.*, (9), **15**, pp. 298-300.

——— 1926. A new lizard from New Caledonia. *Ann. Mag. Nat. Hist.*, (9) **18**, pp. 493-495.

PETERS, W. 1874a. Über neue Reptilien der herpetologischen Sammlung des Berliner zoologischen Museums. *Monatsb. Akad. Wiss. Berlin*, **1874**, pp. 159-164, 1 pl.

——— 1874b. Über einige neue Reptilien. *Monatsb. Akad. Wiss. Berlin*, **1874**, pp. 368-377.

ROUX, J. 1913. Les reptiles de la Nouvelle-Caledonia et des iles Loyalty, in Sarasin and Roux, Nova Caledonia, *Zool.* **1**, pp. 79-160, pls. iv-v.

——— 1930. Note sur un reptile scincide des iles Solomon presetant des pores pediaux. *Verh. naturf. Ges. Basel*, **41**, pp. 129-135, pls.

——— 1934. Contribution a la connaissance de la faune erpetologique des iles Salomon. *Verh. naturf. Ges. Basel*, **45**, pp. 77-81.

SARASIN, F. 1925. Über die Tier geschichte der Lander des Sudwestlichen Pazifischen Ozeans auf Grund von Forschungen in New-Caledonien und auf den Loyalty-Inseln. Nova Caledonia. *Zool.* **4**, Berlin, 1925, pp. 1-127.

SCHMIDT, K. P. 1921. A list of lizards collected by R. H. Beck in the southern Pacific, Nov., 1920 to May, 1921. *Copeia*, No. 101, pp. 90-92.

——— 1922. Second report on lizards secured by the Whitney South Sea Expedition. *Copeia*, No. 104, pp. 23-24.

——— 1923. A list of Fijian lizards. *Copeia*, No. 116, pp. 50-52.

——— 1930. Essay on the Zoogeography of the Pacific Islands in S. N. Shurdift, "Jungle Islands", Putman, New York, pp. 275-292.

SCHMIDT, K. P. and W. L. NECKER. 1933. The Lizards of the Marquesas Islands. *Bernice P. Bishop Mus., Occas. Pap.*, (10) **2**, pp. 1-12, text figs.

SCHNEE, P. 1902. Diek riechtiere der Marshallinseln. *Zool. Gart.*, **43**, pp. 354-362.

SCHUZ, ERNST. 1929. Verzeichnis der Typen des Staatlichen Museums fur Tierkunde in Dresden. 1. Fische, Amphibien und Reptilien mit einen Anhang: Die Schlangender Papuanischen Ausbeut e Dr. Schlagin-thautens 1909. *Abh. Berichte Mus. Dresden*, **17**, 2, pp. 1-16.

SLEVIN, J. R. 1934. Templeton Crocker Expedition to western Polynesian and Melanesian Islands, 1933. No. 15. Notes on the Reptiles and Amphibians, with the description of a new species of Sea Snake. *Proc. Calif. Acad. Sci.* (4) **21**, pp. 183-188.

SMITH, M. A. 1933. Remarks on some old world geckoes. *Rec. Indian Mus.*, **35**, pp. 9-19.

——— 1937. A review of the genus *Lygosoma* (Scincidae: Reptilia) and its allies. *Rec. Indian Mus.*, 39, pp. 213-234.

SNYDER, J. O. 1917. Notes on Hawaiian lizards. *Proc. U.S. Nat. Mus.*, 54, pp. 19-25.

STEINDACHNER, FRANZ. 1870. Herpetologische Notizen. II. Über einige neue oder seltene Reptilien des Wiener Museums. *Sitzb. Akad. Wiss. Wein.*, **61**, pp. 11-25, pls. i-viii.

STEJNEGER, LEONHARD. 1899. The land reptiles of the Hawaiian Islands. *Proc. U.S. Nat. Mus.*, **21**, pp. 783-813.

STERNFELD, RICHARD. 1921. Zur Tiergeographie Papuasiens und der Pazifischen Inselwelt. *Abhandl. Senchenb. Natf. Ges. Frankfurt*, **36**, (for 1920), pp, 375-436, pl. 31.

TANNER. V. M. 1948. Pacific Islands Herpetology, No. 1. Marianas Islands. A new species of Typhlops. *Gt. Basin Nat., Provo, Utah*, **9**, pp. 1-20.

——— 1952. Pacific Islands Herpetology, No. 6, Tahiti and Marquesas Islands, New Guinea and Australia, *Gt. Basin Nat.*, **12**, pp. 1-12.

VISCHER, S. 1925. Tropical cyclones and the dispersal of life from island to island in the Pacific. *Amer. Naturalist*, 59, pp. 70-78

VOGT, THEODORE. 1912. Beitrag zur Reptilien—und Amphibien—fauna der Sudseeinseln. *Sitz. Ber. Ges. Naturf. Freunde, Berlin, Jahrg.* 1912, pp. 1-13.

WERNER, FRANZ. 1899. Beitrage zur Herpetologie der Pacifischen Inselwelt und von Kleinasien. *Zool. Anz.*, **22**, pp. 271-378.

——— 1900. Die Reptilien—und Batrachier—fauna des Biamarck-Archipelo. *Mitt. Zool. Mus. Naturf. Berlin*, bd. **1**, pp. 1-132, figs. 1-46.

November 21, 1953

Presiding: Dr. H. BOSCHMA, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

Secretary: Dr. SILVERIO M. CENDAÑA, College of Agriculture, University of the Philippines, College, Laguna.

PROCEEDINGS

1. Dr. BOSCHMA read his report as Chairman of the Standing Committee on Systematic Zoology.
2. The following papers were read by their respective authors and discussed:
    (a) YUTUC, LOPE M. Arthropod-borne Parasites of the Domestic Animals in the Philippines. (Abstract on page 139 of Abstracts of Papers.)

    (b) GRESSITT, J. L. The Insect Fauna of the Ryukyu Islands. (Abstract on page 142 of Abstracts of Papers.)

    Lantern slides showing the character of the vegetation of the islands where collections were made, were projected and explained by Mr. Walker.

    (c) GRESSITT, J. L. Hispine Beetles of the Coconut Palm. (Abstract on page 142 of Abstracts of Papers.)

    (d) TOWNES, HENRY. Some Mimicry Patterns of Philippine Insects. (Abstract on page 144 of Abstracts of Papers.)

    The paper was accompanied by colored lantern slides showing that insects of similar habit and habitat, even if belonging to different groups, have similar color patterns.

    (e) MCLEOD, J. N. and G. L. AYRE. Parasites of Tent Caterpillars (Lepidoptera: Lasiocampidae) in the Lower Fraser Valley of British Columbia, Canada. (Abstract on page 144 of Abstracts of Papers.)

    (The paper was read by Dr. van Steenburgh in the absence of the authors.)

    (f) KING, K. M. and A. T. S. WILKINSON. European *Agriotes* Wireworms (Elateridae) found established in Coastal British Columbia, Canada. (Abstract on page 143 of Abstracts of Papers.)

(Only the abstract of the paper was read because the authors were absent.)

(g) Bess, Henry A. and Toshiyuki Nishida. Three Fruit Flies (Tephritidae) of Economic Importance in Hawaii. (Abstract on page 145 of Abstracts of Papers.)

(h) Marples, B. J. Spiders in Samoa and the Southwest Pacific.

(The paper was read by title only because the author was not present.

(i) Miller, Robert C. Marine Wood-boring Mollusca of the Philippines. (Abstract on page 146 of Abstracts of Papers).

(j) Turnbull, A. L. Spider Predators of the Spruce Budworm, *Choristoneura fumiferana* (Clem.), at Lillooet, B.C., Canada. (Abstract on page 146 of Abstracts of Papers.)

(The paper was read by Dr. van Steenburgh.)

(k) Herre, Albert W. C. T. The Guitar-Fishes, Family Rhinobatidae, of the Philippines and Adjacent Seas. (Abstract on page 147 of Abstracts of Papers.)

(The paper was read by Dean Uichanco in the absence of the author.)

(l) Watts, B. B. Population Studies and Some Aspects of the Ecology of Potato Aphids in Selected Areas in Canterbury, New Zealand.

(The paper was submitted after the Congress sessions.)

REPORT OF THE STANDING COMMITTEE ON SYSTEMATIC ZOOLOGY

By H. Boschma[1]
Chairman

The Standing Committee on Systematic Zoology was established during the 7th Pacific Science Congress, obviously to stimulate further research in the field of systematic zoology in the vast Pacific area. A great deal of research has been done in this part of the world. Among activities of recent years special mention must be made of the work carried out under the auspices of the Pacific Science Board, which organizes expeditions to various parts of the Pacific, distributes the collected material to specialists of many different groups, and publishes important results, especially in the Atoll Research Bulletin, of which up till now 23 members have appeared.

As Chairman of the Standing Committee for Systematic Zoology it is my duty to deliver to the present Congress a report of the activities of the Committee during the years elapsed since the previous Congress. In this respect the present report is disappointing, for besides mentioning that Dr. C. L. Hubbs (Scripps Institution of the University of California, La Jolla), Dr. M. A. Lieftinck (Zoological Museum, Bogor, Indonesia), and Mr. M. W. F. Tweedie (Raffles Museum, Singapore) accepted the invitation to become members of the Committee, little can be brought forward as facts leading to stimulation of further research. When notwithstanding this I endeavor to deliver a report on systematic zoology of the Pacific, it is to show that our present knowledge of the fauna of this area is not only unsatisfactory, but in many respects so exceedingly fragmentary that for many groups of animals of the Pacific hardly a start has been made for data concerning their occurrence and distribution.

Generally speaking it might be assumed that the study of the marine fauna of the Pacific is in a more advanced state than that of the animals of the land (and fresh water). Because marine animals in their distribution do not appear to be restricted to definite areas, at least not as distinctly as obtains for those living on the land, they lend themselves more easily for generalisation. To illustrate this with an example a few remarks may be given here concerning one of the best known parts of the world, the European region of the Atlantic and the Mediterranean Sea. It is an established fact that a great number of species of many different groups of marine animals occur in the region of the Atlantic coast of Western Europe as well as in the Mediterranean, which often has led to generalisations that later had to be corrected. More detailed studies of animals of various groups have shown that, e.g., certain crustaceans, polychaet worms, and fishes, formerly regarded as of common occurrence in the two regions, now appear to be represented by a distinctly separate species in each of the two. With our increase of knowledge the number of instances of the kind is constantly accumulating.

---

[1] Professor of Systematic Zoology and Director, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

When now I try to demonstrate that our systematic zoological knowledge of the Pacific is far from satisfactory I choose as examples two small well defined groups of animals, systematically of widely different character, and both represented in all the regions in which the Pacific may be divided for comparative studies of the constituents of the fauna. The two groups are the Hydrocorals of the order Stylasterina, and the Crustacean parasites of the order Rhizocephala. The chief reason for choosing these groups is that the present author is sufficiently familiar with the systematics of the animals concerned so that the comparative value of the data in the literature can be taken into account. Notwithstanding the peculiar reason for the selection of the groups, it proved that they lead to striking results when the available data are discussed. A few details concerning the Pacific records of the two groups may be here noted.

Twelve genera of Stylasterina are represented in the Pacific, together containing 127 species or formae occurring in the region. These numbers are almost entirely based on the data from the literature; if the real specimens could be critically examined many of the records would prove to be erroneous, owing to mistakes in identification or to descriptions of new species or formae that in reality have no distinct status.

The Rhizocephala form, as far as concerns their occurrence in the Pacific, a group of a similar size. The Pacific representatives are classified in 22 of the accepted genera, the total number of species reported for the area is 158, among which there are about 10 species of problematic standing or forms with generic identification only.

Small groups as those here mentioned have the advantage that it is not an impossible task to consult the almost complete literature dealing with the various species and their distribution. Exhaustive studies of the literature on Stylasterina from all parts of the world show that the data of any importance are contained in not over 300 publications, from Bosman's description of Guinea on the African coast in 1704 up to the present time. The number of papers dealing with Rhizocephala from all parts of the world is approximately 350. To obtain reliable results on the distribution of the various species of a group of animals the entire literature dealing with representatives of the group must be consulted to avoid mistakes owing to omissions; exhaustive studies of the kind are possible only with small groups of animals. At first the digging up of unimportant looking items in widely scattered literature seems a thankless task, but soon it leads to unexpected results of apparently long forgotten data nicely fitting in into the mass of gradually accumulating records.

The available data of the two groups are here presented in tabular form to facilitate a comparison of the faunal elements of the different regions. It is not intended to regard the regions accepted here as well defined faunal provinces of the Pacific. The division of the area in a number of regions has even been effected in a slightly different manner for each of the two groups, in connection with the available data on occurrence and distribution of the species. The distribution of the Stylasterina in the Central Pacific has, for instance, been noted in some detail, whilst the scanty records of Rhizocephala from the Central Pacific have not been subdivided. On the other hand there are a few records of Rhizocephala from China and from South East Asia, regions from which up till the present not a single Stylasterine coral has become known. Although the data in each of the two tables have been differently combined, the results concerning the two groups are comparable. The two tables show that the fauna of each of the two groups is fairly well known in some of the regions, whilst in other regions the data are altogether insufficient or even completely lacking. When one of the two groups is rather abundantly represented in a certain region, generally also the other appears to be fairly common in this region.

The tables contain the facts on the occurrence of the Stylasterina and of the Rhizocephala as far as known at present. They do not exactly prove that the animals of the two groups in certain regions are fairly common, and rare in other regions; they only prove that research on the fauna has made far greater progress in some of the regions than in many others.

TABLE I

Number of Species and Formae of Stylasterina Occurring in Various Regions of the Pacific.

Stylasterina	Stylaster	Allopora	Stenohelia	Stylantheca	Crypthelia	Conopora	Astya	Distichopora	Errina	Errinopora	Sporadopora	Steganopora	Total
1. Alaska, Bering Sea	4	13			1			1		2			21
2. Okhotsk Sea	1	4								1			6
3. Japan	11	7			2	1		1		1			23
4. Philippine Is.	4				1		1	3					9
5. East Indies	11		3		5	1		2	2			1	25
6. New Guinea	7		1		2	1		2					13
7. Solomon Is.	1							2					3
8. New Hebrides								2					2
9. New Caledonia	1							1					2
10. N.E. and E. Australia	5	1						5			1		12
11. New Zealand	6		1		1	1			6		2		17
12. Canada		3								1			4
13. United States		4		1						1			6
14. Tropical E. Pacific		1	1		4				1				7
15. Chile									2				2
16. Tuamotu Is.	1	1						2					4
17. Society Is.		1						3					4
18. Cook Is.								2					2
19. Samoa Is.	3	1			1			1					6
20. Tonga Is.					1								1
21. Fiji Is.	1				1			3					5
22. Gilbert Is.	1	1						6					8
23. Marshall Is.	2							5					7
24. Caroline Is.	1												1

The tables further give occasion to the following comments:

1. Of the 21 species and forms of infraspecific level reported from the region of Alaska, the Aleutian Islands, and the Bering Sea, 19 are among the best known of all the Stylasterina of the world, owing to the important results obtained by Fisher (1938). Especially the genus *Allopora* is abundantly represented in the region.

2. The occurrence of Stylasterina in the Okhotsk Sea is known from various papers by Broch, of which two, moreover, contain numerous val-

uable data on corals of the group from other parts of the world (Broch, 1936, 1942). In comparison to other regions of the Pacific the Okhotsk Sea is known to contain few species of Stylasterina, but the data concerning these species are reliable.

3. The numerous records for Stylasterina in the Japanese region (23 species or formae) are of highly different value. Many of these are from the older literature so that the specific identifications not always are trustworthy. Of later years there are data by Broch (l. c.), and by Eguchi (1941). A number of records by the last named author, of species not previously known to occur in the region, seem to need confirmation.

In contradistinction to the three regions discussed above, the regions bordering the coasts of Korea, China, Formosa, Indo-China, Thailand, and the Malay Peninsula, have not yielded a single record for the occurrence of Stylasterina. Future research will undoubtedly prove that the study of the corals of the group in this large area up till now has been severely neglected.

4. For the region of the Philippine Islands, including the Sulu Islands and the surrounding parts of the sea, the number of 9 species and formae of Stylasterina does not give an adequate idea of the real conditions. Two species are known from this region only, *Astya subviridis* (Moseley) from deep water, and *Distichopora irregularis* Moseley from shallow water, indicating that the distribution of this species is imperfectly known. The fauna of the Philippine region has not been sufficiently studied to conclude that indeed Stylasterina are of rare occurrence.

5. Of all the here distinguished regions of the Pacific, the East Indies have the largest number of Stylasterina (25 species or formae). Taking into account that 22 of the 25 records are based on the results obtained by the Siboga Expedition (Hickson & England, 1905) it is safe to conclude that the region is one of the best known in the Pacific as far as concerns the fauna of the deeper waters of the sea. On the other hand the three remaining records give an altogether insufficient idea of the occurrence of the corals of the group in the region. Lack of exploration of the reefs and the rocky shores of the numerous islands in the East Indian Archipelago is the cause of the present deficiency of knowledge of shallow water forms in the region.

6. From the region of New Guinea with its adjacent islands, and from the Torres Strait (included in this region for obvious faunistical reasons) 13 species and formae of Stylasterina have become known, the

majority from the collections of the Siboga Expedition which explored a large part of this region too. In this region again the shallow water corals of the group are badly known.

From New Britain, New Ireland, and the Admiralty Islands not a single Stylasterine coral has become known.

7. In the Solomon Islands and the surrounding parts of the sea, three species of Stylasterina are known to occur; a *Stylaster* from comparatively deep water (Studer, 1877), and two species of *Distichopora* from shallow water. The last record available for the region dates from more than seventy years ago, so that new records are badly needed for an insight into the really existing conditions of occurrence of corals of the group.

8. Two species of the genus *Distichopora* have been mentioned as occurring in the New Hebrides (Tenison-Woods, 1879); it is not a generally accepted fact that the two are specifically distinct.

9. One species of *Distichopora* is known to occur off New Caledonia (Gray, 1860); one species of *Stylaster* came from Lifu in the Loyalty Islands. No other records have become available from this region.

10. Northeast and East Autralia, including the Great Barrier Reef. Nine recent species have been reported from this region, among which two are indicated with names that in all probability are synonyms of those of other species also known to occur in the region, thereby reducing the number of species to seven. On the other hand three fossil species were described from Tertiary deposits in Victoria (Hall, 1893, 1898).

From the point of view of marine zoogeography the regions here indicated with the numbers 6–10 may be united into one larger faunal province. By eliminating the extra records of species occurring in two or more of the smaller regions, the total number of species for the larger area then amounts to 21, too small to be regarded as approximately representing the really existing conditions.

11. New Zealand, including the Kermadec Islands and the Chatham Islands. The Stylasterina of this region are better known than those of many other parts of the Pacific, though the number of species and formae (17) does not indicate that the region appears to be exhaustively studied. Some corals of the group from deeper water off the Kermadec Islands were collected by the Gazelle (Studer, 1877) and by the Challenger (Moseley, 1879, 1880), the only species known from the Chatham Islands is a *Sporadopora* from the Upper Eocene (Tenison-Woods, 1880). In the waters around the main islands of New Zealand several species and formae of *Errina* occur (Hickson, 1912), a genus having its chief area of distribution in the Antarctic region.

12 and 13. In the region off the coasts of Canada and the United States one species, *Stylantheca porphyra* Fisher, is restricted to Southern California, the other species are identical with or closely allied to Stylasterina of the Alaska region. Relatively few species have been recorded from the regions here dealt with, probably owing to a comparative rarity of species of the group, certainly not on account of lack of marine research in this part of the world. Included in the total number of species of this region is the fossil coral *Allopora milleri* (Durham, 1942).

From the Pacific coast of Mexico, of Central America, and of South America to the southern part of Chile, not a single species of Stylasterine coral is known.

14. Some collecting has been done by the Albatross in the region of the tropical East Pacific surrounding the Galapagos Islands. The available data point to the fact that this region has a rich fauna of Stylasterine corals, so that the seven species known to live in this region in all probability represent but a fraction of what might become known as a result of further investigation.

15. The region of the Chilean coast. Two species of Stylasterina, both belonging to the genus *Errina*, have been collected in S. W. Chile (Ridley, 1881). The region has not been sufficiently investigated to assume that with these records the corals of the group occuring here are completely known. Zoogeographically the records point to a distinct affinity of the fauna to that of the Antarctic area.

The remaining regions are those of the various groups of islands in the central part of the Pacific, indicated with the numbers 16–24 in the table. The number of species known to occur in each of the groups of island is exceedingly small, the highest numbers are those for the Gilbert Islands (8) and for the Marshall Islands (7) owing to the collecting of material from these islands during Dr. Sixten Bock's expedition in 1907, reported upon by Broch (1936, 1942). When the occurrence of certain species in more than one of the groups of islands is taken into account the complete number of species and formae recorded for the Central Pacific is 22. Even if to this number would be added the data concerning corals of the group in the older literature vaguely indicated as collected in the "South Sea Islands", the total number of Stylasterina known for this vast area would not become much higher. The central Pacific certainly is too insufficiently known to form well founded conclusions on the occurrence and the distribution of the Stylasterine. Moreover, from many groups of islands not a single Stylasterine coral has been mentioned, viz., Marquesas, Austral (Tubuai) Is., Line Is., Phoenix Is., Tokelau Is., Ellice Is., Palau Is., Marianas (Ladrones), and Hawaiian Is. As far as the last named are concerned it is fairly certain that Stylasterina are not represented in the fauna (Edmondson, 1946).

Summarizing the data referred to above we may state that only in a few regions of the Pacific is the occurrence and the distribution of Stylasterina fairly accurately known. In the large majority of the regions, our knowledge of these corals is fragmentary, whilst in many parts of the vast area hardly anything has become known.

The total number of species and formae of Stylasterina reported to occur in the Pacific area is 127. This does not mean, however, that really 127 separate systematic units are known to exist in this part of the world. The descriptions of the various forms are contained in some 40 different papers, many of which are dealing with but one coral of the group, whilst others contain data on several species. Especially in the smaller papers, often species are described as new without comparison of the characters with those of previously described species; many of the described species are of doubtful value, but generally the salient characters are not sufficiently apparent from the description to determine exactly the real status. Only a detailed examination of the material on which the statements in the literature are based might clear the difficulties, but in many instances the material is not easily accessible or no longer exists.

For another reason the specific identification of the Stylasterina reported to occur in the Pacific in many cases needs confirmation before the accepted records can be considered conclusive. Too many Pacific corals of the group have been identified as special that previously were known from the Atlantic only. Now it is an established fact that some species of animals are known from the Pacific as well as from the Atlantic, but most of the records of this kind in regard to Stylasterina need a renewed examination before they may be regarded as well established facts. In his fundamental researches on the Stylasterina of the Challenger Expedition, Moseley (1879, 1880) mentions three species from localities in both the Atlantic and the Pacific, of one of these, *Crypthelia pudica* M. E. & H., the figured specimens are from the Atlantic. Later authors (Hickson & England, 1905; Fisher, 1938) have commented upon the fact that Moseley's species of *Crypthelia* is different from the real *C. pudica.* The difficulty now seems to be entirely solved by assuming that Moseley was not aware of the specific distinction between his specimens from the Pacific and his corals from the Atlantic, and that his figures were made after specimens from the Atlantic belonging to species at that time undescribed.

The Stylasterina of the Siboga Expedition in the East Indian Archipelago and the adjoining parts of the Philippine and the New Guinea regions, were reported upon by Hickson & England (1905). In the material 23 different species were distinguished, 14 of these had to be described as new, 4 were identified as species originally described from the Pacific, 3 as species originally described from the Atlantic, one as a species originally described from South Africa, and finally one as *Stylaster gemmascens* (Esper), of which the original indication of the locality obviously by error, was noted as the East Indies, whilst later the species proved to be of common occurrence in the North Atlantic region. A thorough reexamination of the material of the Siboga Expedition must take place to test the identification of the five last mentioned species; for the present these records remain doubtful. Of one of the species here dealt with, *Stylaster duchassaingi* Pourt., often referred to as *S. eximius* Kent, there are later data concerning its distribution in the Pacific, e.g., by Broch (1936), who compared West Indian material of the species with specimens from Pacific localities, and did not find specific distinctions.

Of the two common species of Stylasterina from the North Atlantic, *Stylaster gemmascens* (Esper) and *Allopora norvegica* (Gunnerus), specimens have been reported from the North Pacific region. A more detailed investigation of material from this region (Broch, 1936; Fisher, 1938) proved that the Pacific representatives of the first named species must be regarded as a separate subspecies *alaskanus* Fisher, the last named as the distinct subspecies *pacifica* Broch.

Common distribution of Stylasterine corals in the Pacific and in the Indian Ocean is more likely than a distribution of species in the Pacific as well as in the Atlantic. With the Indian Ocean, the Pacific forms to a certain extent a faunal unit, many species being known to occur in the two regions. As far as genera are concerned some striking facts may be derived from another group of corals, the *Scleractinia* (Madreporaria), based on data from the comprehensive publication of Vaughan & Wells (1943). Of the 170 recent genera of scleractinian corals, 96 occur in the Indo-Pacific area, 34 are exclusively found in the Atlantic, whilst of the remaining 40 genera 13 occur in the Pacific and in the Atlantic, 7 in the Atlantic and in the Indian Ocean, 12 are known from the three oceans, and 8 have a world-wide distribution. These numbers show that it is rather exceptional for a genus to be distributed in the Pacific as well as in the Atlantic. As far as species are concerned the exception is known to be still greater. This leads to the conclusion that every instance of a record of a species for the two oceans must be regarded as insufficiently founded as long as no definite proof of the identity of the forms from the two areas has become available.

TABLE II

NUMBER OF SPECIES OF RHIZOCEPHALA OCCURRING IN VARIOUS REGIONS OF THE PACIFIC.

	PELTOGASTER	SEPTOSACCUS	PTEROGASTER	DIPTEROSACCUS	BRIAROSACCUS	TEMNASCUS	GEMMOSACCUS	PELTOGASTERELLA	ANGULOSACCUS	LERNAEODISCUS	SEPTODISCUS	TRIANGULUS	TOTAL
1. Japan	4			1				1		1		1	8
3. Philippine Is.			1									1	2
5. East Indies	2	2	2	1						1	1	1	10
6. New Guinea	2	1		1						1	1	1	7
8. North America	3							2	1				6
9. South America					1		1						2
10. Central Pacific						1				1			2

	SACCULINA	DREPANORCHIS	HETEROSACCUS	LOXOTHYLACUS	SESARMAXENOS	CLISTOSACCUS	MYCETOMORPHA	DUPLORBIS	SYLON	THOMPSONIA	SPHAEROTHYLACUS	TOTAL	TOTAL OF THE TWO TABLES
1. Japan	20	2	4	1						2		29	37
2. China	6		1	2						1		9	10
3. Philippine Is.	18		2	2						2		24	26
4. S.E. Asia	7		1									8	8
5. East Indies	38		4	14	1			1			1	59	69
6. New Guinea	10			3						3		16	23
7. East Australia	2											2	2
8. North America			1	1		1	1		1	1		6	12
9. South America				1								1	3
10. Central Pacific	4									1		5	7

The larger part of the papers dealing with the systematics of Rhizocephala are of fairly recent date, so that most of the recognized species are described in such a way that their characters are distinctly known. Moreover, in comparison to the larger number of species known to occur in a restricted area only, there are but a few that have been reported to occur in the Pacific as well as in the Atlantic. In certain cases (Reinhard, 1944) sectioned specimens from the two parts of the world have been accurately compared so that the presence of the species in these two areas is to be accepted.

For an insight in our present state of knowledge concerning the occurrence and the distribution of the Rhizocephala in the Pacific, in Table II the area has been divided into 10 regions, not in every respect corresponding with the regions of the distribution of the Stylasterina contained in Table I. The division in a comparatively small number of regions, however, leads to a useful survey of the group. Some notes concerning the various regions follow here.

1. Krüger (1912) was the first to examine a large number of Rhizocephala from Japan; he gave specific names to several forms, but united the parasites of 9 different species of crabs under the name *Sacculina carcini* Thomps.; none of these has to keep this name. In subsequent papers several other species of the group were described after material from Japan; in a recent publication (Shiino, 1943) again 12 species had to be described as new. The Japanese region now has become one of the best known of the Pacific.

2. China, with Formosa and the adjoining regions of the sea, forms a region of which extremely little is known of occurrence and distribution of Rhizocephala. A few species have become known, obviously a small fragment of the number that in reality occurs in the region.

3. The region of the Philippine Islands, including the Sulu Archipelago, was the first to give occasion to any substantial work on parasites of the group from the tropics. Kossmann's (1872) paper on Rhizocephala from the Philippine Islands was of fundamental importance because for the Sacculinidae he introduced two new principles for the dictinction of specific peculiarities, viz., the morphology of the internal organs, especially of the genital organs, and the characters of the structure of the external cuticle of the mantle. In later papers some more species were added, leading to a total number of 26, so that in this respect the region is much better known than many of the other parts of the Pacific.

4. With a total number of 8 species of Rhizocephala, South East Asia [Indo-China, Siam (Thailand), including the Gulf of Siam, and Malay Peninsula, including Singapore Island] is one of the regions in which very little data on the group have become available. The four records for Siam are based on material collected by Dr. Th. Mortensen in the Gulf of Siam in 1900, most of the records for Singapore Island on material collected by Mr. M. W. F. Tweedie. Examination of numerous specimens from Indo-China, chiefly brought together by Dr. R. Serene, undoubtedly will prove that in the region many more species exist than at present known. The region needs a great deal of further research before a satisfactory result can be achieved.

5. Numerous species of Rhizocephala are known from the East Indian Archipelago, but our knowledge of the animals of the group occurring in this region is still far from exhaustive, not even all the collected material has been sufficiently studied. Besides notes of an incidental character the chief papers dealing with the Rhizocephalan parasites are the results of the Siboga Expedition (van Kampen & Boschma, 1925; Boschma, 1931b), of the Danish Expedition to the Kei Islands (Boschma, 1931a), and of the Snellius Expedition (van Baal, 1937, Boschma, 1940). With its 69 species of Rhizocephala the region has a far larger number of diverse forms of the group than any other part of the Pacific, but to conclude that it is the best known would be beside the truth, because the fauna of the North American coast with its small number of species of Rhizocephala in its entirety is much better known.

6. The region of New Guinea with the Aru Islands and the Torres Straits has records of the occurrence of 23 species of Rhizocephala, a fairly large number, but certainly many more species will be found here as a result of future research. In the Torres Straits important investigations on the anatomy and the life history of a species of *Thompsonia* have been carried out by Potts (1915).

Not a single Rhizocephalan parasite has been reported from the Admiralty Islands, New Ireland, New Britain, the Solomon Islands, the New Hebrides, New Caledonia, and the Loyalty Islands.

7. Very few records are available concerning the occurrence of Rhizocephala in the region of the East coast of Australia; including the Great Barrier Reef. In this region the group is badly in need of further research, which undoubtedly will lead to many hitherto unknown data.

8. North America, from the Bering Sea, the Aleutian Islands and Alaska to South California. Though not especially rich in species (12 have been observed) the region certainly is the best known of all the parts of the Pacific area, chiefly owing to the valuable paper by Reinhard (1944), in which many species are described and others are recorded for the first time as occurring in the region. The new forms include the genus *Angulosaccus* with its peculiar situation of the male genital glands. Previously a few species had become known from California and from the border region of the United States and Canada, including the peculiar aberrant genus *Mycetomorpha* described by Potts (1912).

Not a single species of Rhizocephalan parasites has become known from the region of the coasts of Mexico and of Central America.

9. For the South American coast one *Gemmosaccus,* one *Briarosaccus,* and one *Loxothylacus* have been reported. Probably there are not

many more species of Rhizocephala living in this region, but the fauna is too insufficiently known to regard the present records as conclusive.

10. From all the groups of islands in the Central Pacific no more than 6 species of Rhizocephala have become known, viz., 2 from the Fiji Islands, 2 from the Gilbert Islands, 1 from the Tuamotu Archipelago, and 1 from Hawaii (an unidentified parasite of a Porcellanid, mentioned by Edmondson, 1946). Instead of being an indication of the poverty of the fauna as far as concerns the parasites of the group, these data point to the fact that up to the present hardly a start has been made in the collection of the animals in this vast area.

A summary of the hitherto known facts results in the conclusion that some regions of the Pacific have been rather intensely studied as far as concerns the occurrence and the distribution of Rhizocephala, viz., North America, Japan, Philippine Islands, the East Indies, and New Guinea, whilst in other regions up to the present the records are exceedingly few, viz., for China, S. E. Asia, Australia, South America, and the Central Pacific. Especially in the last named large area as yet hardly a beginning has been made with the study of the group.

It is not intended to maintain that the two small groups of animals dealt with in the previous discussions are representative for the Pacific in so far that the results obtained in these groups are an exponent of the present state of our knowledge of systematic zoology in the various regions of the Pacific. A similar review of other groups of animals undoubtedly would lead to somewhat different results, though it remains a striking fact that the conclusions independently obtained in the two groups of entirely different systematic position are of a corresponding character. We may safely conclude that the regions of the Pacific which in the present paper make a favourable impression are those in which generally the fauna is best known, whilst the reverse holds true for the regions yielding poor results for the two groups dealt with here. Especially the islands in the Central Pacific need a great deal of further research before an adumbration of an inventory of the fauna can be obtained.

REFERENCES

BAAL, I. VAN, 1937. Rhizocephala of the Families Peltogastridae and Lernaeodiscidae. *Biol. Res. Snellius Exp., II. Temminckia*, vol. 2, pp. 1-96, 3 pls., 28 text-figs.

BOSCHMA, H., 1931a. Rhizocephala. Papers Mortensen's Pacific Exp. 1914-16, LV. *Vidensk. Medd. Dansk Naturh. Foren.*, vol. 89, pp. 297-380, 57 text-figs.

———, 1931b. Die Rhizocephalen der Siboga-Expedition. Supplement. Siboga Exp., monogr. 31 bis, 67 pp., 41 text-figs.

BOSCHMA, H., 1940. Some Rhizocephala of the Genus Loxothylacus. *Biol. Snellius Exp., VIII. Temminckia,* vol. 5, pp. 273-372, 65 text-figs.

———, 1953. The Stylasterina of the Pacific. *Zool. Meded. Mus. Leiden,* vol. 32, no. 16, pp. 165-184.

———, 1953. The Rhizocephala of the Pacific. *Zool. Meded. Mus Leiden,* vol. 32, no. 17, pp. 185-201.

BOSMAN, W., 1704. Nauwkeurige Beschryving van de Guinese Goud- Tand- en Slave-Kust, vol. 1. Utrecht, xiv + 207 pp., maps, pls.

BROCH, HJ., 1936. Untersuchungen an Stylasteriden (Hydrokorallen) I. *Skr. Norske Vidensk.-Akad. Oslo, matem.-naturv. Kl.,* no. 8, 103 pp., 13 pls., 52 text-figs.

———, 1942. Investigations on Stylasteridae (Hydrocorals). *Skr. Norske Vidensk.-Akad. Oslo, matem.-naturv. Kl.,* no. 3, 113 pp., 6 pls., 38 text-figs.

DURHAM, J. W., 1942. Eocene and Oligocene Coral Faunas of Washington. *Journ. Paleont.,* vol. 16, pp. 84-104, pls. 15-17, 1 text-fig.

EDMONDSON, C. H., 1946. Reef and Shore Fauna of Hawaii. *Bernice P. Bishop Mus., Special Publ.* 22, 381 pp., 223 text-figs.

EGUCHI, M., 1941. Stylasterinae from Japanese Seas. *Jubilee Publ. Prof. H. Yabe,* vol. 2, pp. 1171-1194, 1 pl.

FISHER, W. K., 1938. Hydrocorals of the North Pacific Ocean. *Proc. U.S. Nat. Mus.,* vol. 8, pp. 493-554, pls. 34-76.

GRAY, J. E., 1860. Description of a New Species of Distichopora from New Caledonia. *Proc. Zool. Soc. London,* pp. 244-245, Radiata pl. xvii.

HALL, T. S., 1893. On two new Tertiary Stylasterids. *Proc. Roy. Soc. Victoria* (n. s.), vol. 5, pp. 117-122, pl. xiii.

———, 1898. Stylasteridae from the Victorian Tertiaries. *Proc. Roy. Soc. Victoria* (n. s.), vol. 10, pp. 175-179.

HICKSON, S. J., 1912. On the Hydrocoralline Genus, Errina. *Proc. Zool. Soc. London,* pp. 876-896, pls. xciv-xcvi.

HICKSON, S. J. and H. M. ENGLAND, 1905. The Stylasterina of the Siboga Expedition. Siboga Exp., monogr. 8, 26 pp., 3 pls.

KAMPEN, P. N. VAN and H. BOSCHMA, 1925. Die Rhizocephalen der Siboga-Expedition. Siboga Exp., monogr. 31 bis, 62 pp., 3 pls., 45 text-figs.

KOSSMANN, R., 1872. Beiträge zur Anatomie der schmarotzenden Rankenfüssler. *Inaug.-Diss. Würzburg,* 43 pp., 3 pls. (also in: *Arb. Zool.-zoot. Inst. Würzburg,* vol. 1, 1874, pp. 97-137, pls. v-vii).

KRUGGER, P., 1912. Über Ostasiatische Rhizocephalen. *Abh. math.-phys. Kl. K. Bayer. Akad. Wiss.,* suppl.-vol. 2, 16 pp., 3 pls., 13 text-figs.

MOSELEY, H. N., 1879. On the Structure of the Stylasteridae, a Family of the Hydroid Stony Corals. *Phil. Trans. Roy. Soc. London,* vol. 169, pp. 425-503, pls. 34-44.

———, 1880. Report on Certain Hydroid, Alcyonarian, and Madreporarian Corals Procured during the Voyage of H. M. S. Challenger, in the Years 1873-1876. *Rep. Sci. Res. Challenger, Zoology,* vol. 2, (Hydrocorallinae, pp. 11-101, pls. 1-14).

POTTS, F. A., 1912. Mycetomorpha, a New Rhizocephalan (with a Note on the Sexual Condition of Sylon). *Zool. Jahrb., Syst.,* vol. 33, pp. 575-594, pls. 15-16, 12 text-figs.

POTTS, F. A., 1915. On the Rhizocephalan Genus Thompsonia and Its Relation to the Evolution of the Group. *Carnegie Inst. Washington, Publ.* 212, pp. 3-32, 2 pls., 12 text-figs.

REINHARD, E. G., 1944. Rhizocephalan Parasites of Hermit Crabs from the Northwest Pacific. *Journ. Washington Acad. Sci.*, vol. 34, pp. 49-58, 7 text-figs.

RIDLEY, S. O., 1881. Coelenterata. Account of the Zoological Collections Made during the Survey of H.M.S. "Alert" in the Straits of Magellan and on the Coast of Patagonia. *Proc. Zool. Soc. London*, pp. 101-107.

SHIINO, S. M., 1943. Rhizocephala of Japan. *Journ. Sigenkagaku Kenkyusyo*, vol. 1, pp. 1-36, 24 text-figs.

STUDER, TH., 1877. Uebersicht der Steinkorallen aus der Familie der Madreporaria aporosa, Eupsammina und Turbinaria, welche auf der Reise S. M. S. Gazelle um die Erde Gesammelt Wurden. *Monatsber. k. Preuss. Akad. Wiss. Berlin*, pp. 625-655, 4 pls.

TENISON-WOODS, J. E., 1879. On the Anatomy of Distichopora—with a Monograph of the Genus. *Journ. Proc. Roy. Soc. New South Wales*, vol. 13, pp. 49-63, 2 pls.

————, 1880. Corals and Bryosoa of the Neozoic Period in New Zealand. *Palaentology of New Zealand*, pt. 4. Wellington, xvi + 34 pp., 3 pls., 1 text-fig.

VAUGHAN, T. W. and J. W. WELLS, 1943. Revision of the Suborders, Families, and Genera of the Scleractinia. *Geol. Soc. America*, Special Papers no. 44, xv + 363 pp., 51 pls., 39 text-figs.

WELTNER, W., 1898. Cirripedien. *Hamburger Magelhaensische Sammelleise*, pt. 4. Hamburg, 16 pp.

ARTHROPOD-BORNE PARASITES OF THE DOMESTIC ANIMALS IN THE PHILIPPINES

By L. M. Yutuc
College of Veterinary Medicine
University of the Philippines
Quezon City, Philippines

Perhaps the earliest evidence on the role of arthropods as transmitters of parasites was that of Melnikov (1869), who demonstrated the larval form of *Diphylidium caninum* in the body cavity of such a host, the dog louse, *Trichodectes canis,* infected experimentally. Grassi and Rovelli (1888) showed the larval stage of *Hymenolepis diminuta,* the cysticecoid developed in the body cavity of a large number of mealworms. However, not until Smith and Kilborne (1893) had demonstrated that ticks transmitted a protozoan disease, Texas cattle fever, and Ross (1898) showed that a female mosquito could transmit bird malaria, that a general interest on the subject have received world-wide attention. In a list of arthropod hosts of worms alone, Hall (1929) recorded no less than 271 species of arthropods serving as intermediate hosts of 143 worms in general. It is not unlikely that the list has been greatly augmented in recent times. In fact, domestic animals share their parasites more with arthropods than with any other group including man due to a great extent to the numerical superiority of arthropods over all known species of animals.

As far as can be ascertained the earliest investigations on the arthropod vectors in the Philippines were the transmission experiments of Banks (1907) and Mitzmain (1912; 1913). The former worked on malarial transmission experiments using *Myzomia ludlowei.* The latter found the stablefly, *Stomoxys calcitrans* a negative factor, but the horsefly, *Tabanus striatus,* positive and principal vector of *Trypanosoma evansi,* the etiological agent of the disease commonly known as surra. The principal object of this paper is to report the present status of the arthropod-borne parasites of the domestic animals in the Philippines. In this article the term arthropod embraces insects and its allies belonging to the phylum Arthropoda.

PROTOZOAN PARASITES

In general the protozoan fauna of the domestic animals in the Philippines has not been adequately investigated. To some extent, this is one of the reasons which accounts for the paucity of literature dealing with this group of parasitic organisms. A review of the literature credited investigators with some twenty species of protozoa recorded from Philippine domestic animals (Table I). Of this number reported seven are recognized as arthropod-borne, namely *Trypanosoma evansi, T. theileri, Haemoproteus columbae, Plasmodium gallinaceum, Bebesia bigemina, B. canis* and *Anaplasma marginale.* In this paper, for obvious reasons, only *Trypanosoma evansi* and *Bebesia canis* are discussed at some length. In the other five species it seems sufficient to indicate the arthropod involved as seen in Table I.

Trypanosoma evansi (Steel, 1885).—This monomorphic flagellate is roughly serpentine-like in shape (Plate I, Fig. 1). While the posterior extremity is frequently triangular, it may be blunt in form at times; the body tapering gradually towards the anterior end. The nucleus is oval or rounded and situated about the middle of the body with a bluish pink tinge in blood films stained with Wright's stain. In the cytoplasm there are no distinct granules in front of the nucleus. Occasionally, however, but few are found and these are not deeply stained either. For the most part these granules are found behind the nucleus and are deeply stained. They are known as volutin granules. The kinetoplast consisting of the blepharoplast and the parabasal body is located a short distance from the posterior end of the parasite. From it arises the undulating membrane, which is thrown into two or three and rarely five graceful folds as it courses anteriorly until the free flagellum. The organism measures from 18.34 to 30.00 by 0.164 to 3.50 microns in general. The size varies not only with the species of the host but also with the stage of infection in the same individual. The trypanosome is moderately motile in wet blood film, the undulating membrane and the flagellum being the organs mainly responsible for its active movements.

The organism is a blood intercellular parasite of the horse, dog, cattle and the water buffalo in the Philippines. Its occurrence is quite common. All mammalian laboratory animals are susceptible to it. Birds to some degree can also be infected.

Although as early as 1901, the mode of transmission of *Trypanosoma evansi* have been ascribed to be through the bite of some suctorial insects, probably either a fly or a mosquito (Smith, 1901), it remained for Mitzmain (1913) to determine the insect involved in the spread of the organism of surra. In a series of carefully planned experiments it was demonstrated that the horsefly, *Tabanus striatus* is the principal vector of the parasite. Moreover, in the collected studies on the insect transmission experiments the same investigator (1914) listed the following insects: *Aedes* (*Stegomyia*) *Calopus, Culex fatigans, Lyperosia exigua, Philaematomyia crassirostris, Hippobosca maculata, Culicoides judicaudus, Phlebotomus* sp., and *Musca domestica* as negative vectors, while horsefly, *Tabanus striatus* have been confirmed as potential and principal transmitting agent of the parasite (Plate I, Fig. 2). Recent experiments, however, showed the housefly could transmit surra trypanosome (de Jesus, 1951).

Inspired principally with the idea of determining a cyclic development of the trypanosome in the body of the arthropod vector, Kelser (1927) conducted a series of transmission experiments using horsefly, *Tabanus striatus*, mosquito, *Aedes aegypti*, two species of ticks, *Boophilus* (*australis*) *microplus, Rhipicephalus* (*D. variabilis*) *sanguineus*, stable fly, *Stomoxys calcitrans* and *Lyperosia exigua*. Although two positive results were obtained with the mosquito, *Aedes aegypti*, the author concluded in part from his results that the common disseminating agent of surra among animals of the equine species in the Philippines at least is *Tabanus striatus*. Since no evidence of cyclic changes in the body of the vector was observed, the mode of transmission is purely mechanical (Plate I, Fig. 4).

Yutuc (1950) repeated the transmission experiments of the above cited investigators employing two species of horseflies, *Tabanus reducens* and *Tabanus striatus*. Positive results were recorded in both insects. However, from the results presented *Tabanus reducens* (Plate I, Fig. 3) appeared to be a more efficient vector than *Tabanus striatus* due probably to its bigger size, indirectly supporting the mechanical means of transmission as elsewhere advanced.

Bebesia canis (Piana and Galli-Valera, 1895).—This is an intracellular protozoan parasite. The typical pear-shaped organism measures about 4.5 to 5 microns in length, pointed at one end and rounded and bulb-like at another (Plate I, Fig. 5). The cytoplasm is generally vacuolated. In dried stained films of blood, the nucleus consists of deeply staining granules closed to the pointed end and extending from it is a string of finer chromatinic granules. Although the parasite is pear-shaped in its typical form, it may appear in a number of forms depending largely on its stage of asexual development. Multiple infections of the red blood cells from 4 to 16 parasites are frequently observed.

The arthropod host has not been studied carefully in the Islands due largely to its uncommon occurrence of the organism. St. John, Simmons and Reynolds (1931) demonstrated in two experiments that the common dog tick, *Rhipicephalus sanguineous* is able to transmit the organism from infected to clean dogs with a 5-day prepatent period (Plate I, Fig. 6). In the invertebrate host the organism undergoes sexual cycle. It was further shown in the experiments that the virulence of the parasite decreases with the age of the mammalian host.

Metazoan Parasites

From the summary of the parasitic worms reported from the Philippines covering a period of 70 years up to 1946 there are listed some 336 species from mammals, birds, reptiles, amphibians, fishes, arthropods and snails (Tubangui, 1947). From the above figures together with those that appeared after 1946 there are 161 helminths reported from the domestic animals of the country. Twenty three of these are reported to spend part of their life cycles in arthropods. Excluding those that are described in the foregoing with their respective intermediate hosts in brackets, these are: *Monieza expansa* (oribatid mites of the genus *Galumna*), *Raillietina tetragona* and *R. echinobothrida* (ants of the genera *Tetramorium* and *Pheidole*), *Diphylidium caninum* (fleas, *Ctenocephalides felis, C. canis* and lice, *Trichodectes canis*), *Habronema majus* (stablefly, *Stomoxys calcitrans*), *H. muscae* and *H. megastoma* (housefly, *Musca domestica*), *Ascarops strongylina* (beetles, *Aphodius rufus, A. lividus, A. granarius* and *Passalus cornutus*), *Physocephalus sexalatus* (dung beetles, *Ataenius cognatus, Passalus cornutus, Copris minutus, Canthon pilularius, Phanaeus carnifix, P. vindex,* etc.), *Gongylonema ingluvivola* (beetles), *Spirocerca lupi* (beetles, *Scarabaeus sacer, S. variolosus, Akis goryi, Geotrupes douei, Copris hispana, Gymnopleurus sturmi* and *Canthon* sp.), *Physaloptera praeputialis* (German cockroach, *Blatella germanica,* camel cricket, *Centophilus* sp., and the common field cricket, *Gryllus assinilis*), *Thelazia rhodesi* (*Musca larvipara* and *M. autumnalis*), *Oxyspirura mansoni* (cockroach, *Pycnocelus surinimensis*), *Setaria cervi* (stablefly, *Stomoxys calcitrans*) and *Macracanthorhynchus hirudinaceus* (June beetle, *Citinus nitida* and May beetle, *Phyllophaga* sp.)

Paragonimus westermanii (Kerbert, 1878) Baun, 1899.–Along with 17 cases in man, Musgrave (1907) reported the fluke in the lung tissue of one of the 32 native cats autopsied. The trematode is mainly confined in certain localities in the southern provinces of Luzon. According to Tubangui (1946) the second intermediate host is a river crab, *Parathelphusa mistio* (Plate II, Fig. 8). The young fluke is encysted in the muscles of the legs, in the gills, liver and thoracic muscles. The encysted metacercarae are double-walled, the inner 300 to 320 and the outer wall 340 to 400 microns, globular and whitish. The first intermediate host is a snail, *Brotia asperata* (Tubangui, Cabrera and Yogore, 1950). The adult recovered after artificial infection of rats and cats developed into matured lung flukes morphologically indistinguishable from the adult Paragonimus of local origin.

This lung fluke has been described as variable in shape and size, but it is generally oval. Its color ranges from light slate to dark reddish brown. The cuticle is rather thick, ornated with spines. The anterior and ventral suckers are spherical to oval in outline, the latter being slightly larger than the former and located slightly anterior to the equator of the fluke. The pharynx is constricted and leads to a short oesophagus, the latter dividing into two caeca coursing posteriorly in a zigzag pattern. The genital pore is small, often indistinct. The male organs are not well developed; branched testis lie in each side of the median line. Female organs are rather short, compact closely coiled uterus, lying on either of the median line posterior to the ventral sucker; ovaries are distinct and branched. Excretory pore is prominent, situated at the posterior end. Vitellaria are numerous, well developed covering almost the entire worm (Plate II, Fig. 9). Eggs are operculated, oval, light to reddish brown color and measure 85 to 100 by 50 to 60 microns (Plate II, Fig. 7).

Diphyllobothrium erinacei (Rudolphi, 1819).—This worm is commonly known as Manson's tapeworm, reported for the first time in the country by Wharton (1917). It has an incidence of 3.3 and 0.4 percent in the cat and the dog respectively. The scolex is spindle-shaped and measures 0.19 by 0.06 mm. with a dorsal and ventral bothriae (Plate III, Fig. 11). The entire worm measures 40 to 62 centimeters long; segment 2 to 3 by 7 to 11 mm. (Plate III, Fig. 12); eggs 58.6 to 68.0 by 34 to 41.6 microns (Plate III, Fig. 14). According to Africa (1934) two local species of copepods, *Cyclops serratus* and *C. bicolor,* are suitable intermediate hosts (Plate III, Fig. 13). Sixteen days after infection the larval tapeworm reached its infective stage, the procercoid (Plate III, Fig. 10). The second intermediate hosts are various species of frogs. These are infected during the tadpole stage. In the frogs, the procercoid developed into plerocercoid commonly known as sparganum. Besides, a species of toad, *Bufo merinus,* a bittern and a snake were found naturally harboring the sparganum. Ira-Concepcion (1935) reported its occurrence in the connective tissue of a student residing in Manila. Sparganosis in the human subject in the Orient is generally ascribed to the plerocercoid of *Diphyllobothrium erinacei.*

Gnathostoma spinigerum (Owen, 1836).—As far as can be ascertained this species is one of the two nematodes first described in the country. It was reported from a palm civet (Schneider, 1886). While it is a common worm of the domestic cat with an incidence of almost 40 percent, in the dog its incidence is only about 7 percent. The male measures

10 to 25 by 1 to 1.5 mm.; female 9 to 31 by 2 to 2.5 mm. The head-bulb is large with four submedian cavities (ballonets) which each communicates with a cervical sac (Plate III, Fig. 15). The cuticle of the head-bulb is armed with 6 to 11 transversed rows of hooks, while the anterior two-thirds of the body bears large, flat, cuticular spines with dentriculate posterior edges. The ventral caudal region of the male bears spines and 4 pairs of large pendaculate papillae together with a number of sessile ones (Plate III, Fig. 16). The left spicule is 1.1 to 2.63 mm., the right 0.4 to 0.8 mm. long. Eggs are oval with a cap at one pole, measure 69 by 27 microns (Plate III, Fig. 17). In a case of parasitic purulent peritonitis in a cat, the eggs were also encountered in the peritoneal exudate together with many adult gnathostomes.

Refuerzo and Garcia (1938) infected two species of cyclops, *Cyclops serratus* and *Cyclops bicolor* with eggs of *Gnathostoma spinigerum* from which the larvae developed after a number of days (Plate III, Fig. 18) thus confirming the previous investigation of Prommas and Daengsvang (1933). The second intermediate hosts are various species of fresh water fishes, *Ophiocephalus striatus, Therapon argenteus* and *Glossogobius giurus* (Africa, Refuerzo and Garcia, 1936). A number of accidental infections in man have been reported in the Orient especially in Thailand.

Cheilospirura hamulosa (Diesing, 1851).—This species is found in the musculature of the gizzard of chicken with an incidence of 8 to 13 percent. The male measures 8.5 to 12 by 0.3 mm.; female 21.5 to 23.5 by 0.5 mm. The body is provided with four double cuticular cordons extending from the cephalic end to, sometimes beyond, the posterior sixth of the body length; do not anastomose. Mouth with two conical lips, each with two papillae. Oesophagus approximately one-third of the body length (Plate IV, Fig. 22). Spicules dissimilar; right shorter but broader; left one longer but narrower. Caudal alae weakly developed. There are ten pairs of stalked genital papillae, 4 pairs preanal and 6 postanal (Plate IV, Fig. 23). Cloacal opening is about 0.6 to 0.7 mm. from the tail tip. In female vulva is behind middle of the body. Eggs are embryonated when layed with smooth thick shell, 43 to 45 by 24 to 25 microns (Plate IV, Fig. 19).

Alicata (1938) found a wide variety of arthropod hosts, consisting of grasshoppers, sandhoppers, flour and manure beetles as well as rice and other grain beetles. In the Philippines Refuerzo (1940) reported two species of grasshoppers, *Aeolopus tamulus* and *Oxya sinensis* which served as intermediate hosts (Plate IV, Fig. 21). The larvae recovered from the grasshoppers measure 0.72 by .06 mm.; tail with four digit-like processes (Plate IV, Fig. 20).

In one instance the adult worm was recovered under the conjunctival mucus membrane of man producing a chronic catarrhal inflammation (Africa and Garcia, 1936).

Dirofilaria immitis (Leidy, 1856).—This worm inhabits mainly the right ventricle of the heart and the pulmonary arteries of the dog, hence the common name heart-worm. In one instance one male and one female adult worm were recovered from the hepatic artery. In 77 dogs examined by ordinary wet covered glass blood preparation, 7 dogs were positive or an incidence of 9 percent. In another survey using autopsy, out of 50 dogs 9 were found positive or an incidence of 18 percent. The male worm measures 145 to 180 by 0.7 to 1 mm.; female 200 to 315 by 1 mm. The anterior extremity is rounded, lipless and with a very small mouth ornated by 6 inconspicuous papillae (Plate V, Fig. 25). The oesophagus is relatively short, divided into an anterior muscular and a posterior glandular portion. The posterior end of the male is spirally coiled into two to three coils with small caudal alae and terminates bluntly (Plate V, Fig. 26). There are generally 11 pairs of caudal papillae of which 6 are postanal. The spicules are dissimilar in length, right 175 to 211 microns; left 300 to 355 microns. Gobernaculum is wanting. The vulva is located 2.6 mm. from the anterior extremity. The larvae hatch from the ova before escaping from the vulva and possess no sheath (Plate V, Fig. 24). They are referred to as microfilariae.

The microfilariae are found in the blood stream of infected animals, are quite motile and measure 218 to 329 by 5 to 6 microns. The anterior end is bluntly rounded while the posterior is pointed and devoid of nuclei near the tip of the anterior extremity. There is a slight microfilarial periodicity, slightly more numerous at night than in the day. The microfilariae have also been encountered in the ascitic fluid.

Various species of mosquitoes serve as intermediate hosts. The dog, cat and human fleas may also act as intermediate hosts. In the Islands, del Rosario (1936) found two species of mosquitoes as suitable intermediate hosts, namely *Culex quinquefasciatus* and *Stegomyia fasciata* with a microfilariae infection of 72.4 and 73.4 percent, respectively (Plate V, Fig. 27). The microfilariae burden is thus more in *Stegomyia fasciata* than in the *Culex quinquefasciatus.*

About 8 to 9 months are essential for the appearance of mature worms in the heart and pulmonary arteries after an infective bite of a microfilariae infected mosquito. Moreover, the microfilariae undergo a period of development in the intermediate host before infection of the dog is possible.

Dispharynx nasuta (Rudolphi, 1819) Stiles and Hassall, 1920.—This spiral stomach worm is found in the proventiculus of fowls. The body is usually coiled into a spiral with 4 wavy bands from the anterior end and extending posteriorly as far as, or anterior of the level of, the oesophagus (Plate VI, Fig. 28). The male measures 4.5 to 8.3 by 0.3 to 0.5 mm; the female 5.5 to 10.2 by 0.5 to 0.56 mm. In the male, there are 9 pairs of caudal papillae, 4 pairs preanal and 5 postanal (Plate VI, Fig. 30). Spicules are unequal; right boat-shaped, short but wide, 0.15 to 0.20 mm; left filiform, 0.45 to 0.52 mm. The vulva is located anterior to the equator of the body. The eggs are embryonated when deposited with 0.033 to 0.035 by 0.018 to 0.025 mm. (Plate VI, Fig. 29).

Tetrameres fissispina (Diesing, 1860).—This globular stomach parasite of chicken is found in the walls of the proventiculus, characterized by marked sexual dimorphism. The male is thread-like, whitish and possesses along each lateral and median aspects a single row of posteriorly directed small spines, extending from behind the buccal cavity to behind the level of the cloacal opening (Plate VI, Fig. 33). It measures 3.48 to 5 by 0.09 to 0.20 mm. Buccal cavity is present but short with 3 lips, each with terminal papilla; oesophagus is composed of a slender muscular anterior part and a glandular posterior segment. The spicules are unequal; right short, sharp-pointed 0.115 to 0.140 by 0.004 mm.; left thick with rounded end, 0.310 to 0.320 by 0.015 mm. The female measures 1.67 to 6 by 1.08 to 3.5 mm. Body subglobular, blood-red with slender cephalic and caudal extremities, transversely striated with four longitudinal depressions correspondingly to median and lateral lines Plate VI, Fig. 32). The anterior extremity protruded from the globular body for about 1.2 mm. and the posterior end for about 0.5 to 0.9 mm. Both are movable and more or less retractile. The vulva is at the junction of the posterior extremity with the body. The deposited eggs are embryonated, oval with smooth thick shell, 0.048 to 0.056 by 0.025 to 0.030 mm. (Plate VI, Fig. 34).

Infection experiments of chicks with nematode larvae obtained from pill bugs.—On March 10, 1946 twenty pill bugs. *Armadillium* sp., were dissected (Plate VI, Fig. 31). Twelve were positive of nematode larvae, the range of infection being one to three larvae with a total of 20 larvae. These were fed to two clean nine-day old chicks, which were raised off the ground and kept in a screened cage to preclude extraneous infection. Five days later one of the chicks died and on autopsy two immature female *Tetrameres fissispina* and one immature *Dispharynx nasuta* were collected from the proventiculus. On April 3, 1946 or 24 days after infection the other bird died; autopsy revealed one mature *Tetrameres fissispina* embedded in the wall of the proventiculus.

Of forty pill bugs dissected on March 17, 1946, 14 were positive with 14 larvae. These were immediately given to a third chick, which died the day following. In the postmortem examination one larvae was recovered from the crop. On March 24 an additional 34 pill bugs were examined with 19 positive. Of the positive bugs, one was infected with five, two with two each and the rest one larvae each, with a total of 25 larvae collected. All were fed to a fourth chick. Six days later the chick was noted weak and killed in extremis. Eleven immature *Dispharynx nasuta* were recovered from the proventiculus. The cephalic cordons were already clearly noted in the specimens collected.

From the meagre results thus far obtained it seems reasonable to state that pill bugs, *Armadillium* sp., act as intermediate hosts of *Dispharynx nasuta* and *Tetrameres fissispina* in this country. This finding lends added support to the observation in the United States where sow bugs, *Porcellio scaber* and pill bugs, *Armadillium vulgara* serve as intermediate hosts of *Dispharynx nasuta.* In Europe an amphipod, *Gummarus,* a clodoceran, *Daphnia,* and several species of grasshoppers, cockroaches and earthworms were found to serve as intermediate hosts of *Tetrameres fissispina* (Morgan and Hawkins, 1951). It appears from the above-mentioned intermediate hosts that this is the first time a pill bug has been incriminated intermediate host of *Tetrameres fissispina.*

Host-Parasite Relationship

One of the important relationships of the parasites with the vertebrate hosts is through the role played by arthropods as intermediary agents. Such a relation varies in degree in different species of parasites, the simplest being that of a mechanical medium between the parasite and the final host, no changes taking place in the body of the arthropod. As a rule the parasite does survive only for a short time in the body of the vector. This simple relation in the life cycle of the parasite finds an example with *Trypanosoma evansi* in its spread in nature through the agency of various species of Tabanid flies resulting from their feeding habits from one animal to another. The multiplication of the trypanosomes occurs in the final hosts such as the horse, dog, cattle, carabao, etc. In *Bebesia canis* of the dog, the relationship follows a complex turn of events, because the parasite multiplies not only in the final host but also in the intermediate host, the tick, and because developments take place in both hosts, in the former asexual and the latter sexual cycle. The infection in the tick is also transmitted to its progenies. Such a state of biological behavior is cyclo-propagative, that is the organism undergoes cyclic changes and multiplies in the arthropod involved. In view of the above circumstance, there is the possibility that some of the parasites of animals may have been parasites of arthropod originally and that their ingress to animals may have been a recent acquired character when the arthopods become parasitic upon vertebrates.

A more restricted and delicate relationship but less complicated exists in certain metazoan helminths. For instance, the heart-worm of the dog. *Dirofilaria immitis* the larval stage, microfilaria once taken into the body of the mosquito with the blood meal, it is obligated to develop before the definitive host, the dog can be infected by the bite of a mosquito bearing infective microfilariae. The above behavior is cyclo-developmental, that is, the parasite undergoes cyclic changes but does not multiply. Unlike the two cited protozoa, the complete cycle is always tri-dimensional. Moreover, in spite of the biological dissimilarity between *Trypanosoma evansi* and *Bebesia canis* in the body of their respective arthropod hosts, both can be maintained in the laboratory without the intervention of an arthropod.

What is true in the parasite relation of *Dirofilaria immitis* is shared by the other metazoan parasites described briefly in this paper except in *Paragonimus westermanii, Diphyllobothrium erinacei* and *Gnathostoma spinigerum.* In the former, in addition to the arthropod host, the river crab, the initial stage in the development of the fluke occurs in the snail before the crab can take its role in the life cycle of the parasite. On the other hand, in the latter two, *Diphyllobothrium erinacei* and *Gnathostoma spinigerum,* the cyclop constitutes the first intermediate host for both, the second intermedite hosts being fresh water fishes for the latter and frogs for the former, before both can infect the vertebrate hosts. Further, the pleroceroid (sparganum) of *Diphyllobothrium erinacei* have been reported in nature in a number of hosts; and in the Philippines these are snake, bittern and even man. Almost all laboratory animals from chicken to monkey except fresh water fishes can take the infection without change in form. Such an adjustment of the larval parasite is remarkable. In general, these are considered auxillary hosts of Manson's tapeworm. In the three mentioned helminths, the relationship is four-sided and is obligatory but falls under the category mentioned for *Dirofilaria immitis,* the arthropod concerned plays only a part but essential in the life cycle of the parasite.

Lastly, such relationship brought out in the above discussion between the parasite on one hand and the vertebrate host on the other through the agency of arthropods is too obvious to emphasize in the control and prevention of parasitism in general. Finally, the ability to transmit parasitic diseases of animals to a great extent is directly related to the structure, physiology and habits of the arthropods involved.

SUMMARY

A brief discussion of the parasites of domestic animals in which the vectors or intermediate hosts have been studied in the Philippines is presented. Of the twenty protozoan parasites recorded, seven are arthropod-borne, namely *Trypanosoma evansi, T. theileri, Haemoproteus columbae, Plasmodium gallinaceum, Bebesia bigemina, B. canis* and *Anaplasma marginale.* Only the vectors of *T. evansi* and the intermediate host of *Bebesia canis* have been determined. The former are horseflies, *Tabanus striatus* and *T. reducens* and the latter ticks, *Riphicephalus sanguineous.*

With 161 metazoan parasites reported affecting native domestic animals, 23 spent part of their life cycle in arthropods. These are *Paragonimus westermanii, Monieza expansa, Raillietina tetragona, R. echinobothrida, Diphylidium caninum, Diphyllobothrium erinacae, Habronema megastoma, H. muscae, H. majus, Ascarops strongylina, Physocephalus, sexalatus, Gongylonema ingluvicola, Gnathostoma spinigerum, Spirocerca lupi, Physaloptera praeputialis, Thelazia rhodesi, Oxyspirura mansoni, Cheilospirura hamulosa, Dirofilaria immitis, Dispharynx nasuta, Tetrameres fissispina, Setaria cervi* and *Macracanthorhynchus hirudinaceous.* However, it is only in seven species where the arthropods involved have been worked out. With their corresponding arthropod hosts, these are *P. westermanii,* fresh water crab (*Parathelphusa mistio*); *Diphyllobothrium erinacei* and *Gnathostoma spinigerum,* cyclops, (*Cyclops serratus* and *C. bicolor*); *Cheilospirura hamulosa,* grasshoppers, (*Aeolopus tamulus* and *Oxya sinensis*); *Dirofilaria immitis,* mosquitoes, (*Culex quinquefasciatus* and *Stegomyia fasciata*); *Dispharynx nasuta* and *Tetrameres fissispina,* pill bug, (*Armadillium* sp.), the last two nematodes being reported as arthropod-borne for the first time in the Philippines.

The arthropod role in the vertebrate host-parasite relationship is discussed.

REFERENCES

AFRICA, C. M. Experimental infection of Philippine cyclops with coracidia of *Diphyllobothrium mansoni* Cobbold, 1882. *Phil. Jour. Pub. Health.* I (1934) 27-31.

AFRICA, C. M., F. J. DY and L. J. SORIANO. A study on the identity of a Plasmodium in the Philippine domestic fowl (*Gallus gallus*). *Univ. Phil. Nat. and Appl. Sci. Bull.* 7 (1940) 279-284.

AFRICA, C. M. and E. Y. GARCIA. A new nematode parasite (*Cheilospirura* sp.) of man in the Philippines. *Jour. Phil. Is. Med. Assoc.* 16 (1936) 603-607.

AFRICA, C. M., P. G. REFUERZO and E. Y. GARCIA. Observations on the life cycle of *Gnathostoma spinigerum*. *Phil. Jour. Sci.* 59 (1936) 513-523.

————, P. G. REFUERZO and E. Y. GARCIA. Further observations on the life cycle of *Gnathostoma spinigerum*. *Phil. Jour. Sci.* 61 (1936) 221-225.

ALICATA, J. E. The life cycle of the gizzard worm (*Cheilospirura hamulosa*) and its mode of transmission to chicken with special reference to Hawaiian conditions. *Libro Jubilar de Prof. L. Tuavassos.* (1938) 11-20.

BANKS, C. S. Experiments in malarial transmission by means of *Myzomia ludlowei* Teob. *Phil. Jour. Sci.* 2 (1907) 513.

CORONEL, A. B. Avian malaria of pigeons. *Phil. Jour. Ani. Ind.* 4 (1937) 205-207.

CRAM, E. B. Developmental stages of some nematodes of the Spiruroidea parasitic in poultry and game birds. *Tech. Bull. No. 227. U.S. Dept. Agri.* (1931) 1-28.

DE JESUS, ZACARIAS. The occurrence of blackheads in turkeys in the Philippines. *Phil. Jour. Ani. Ind.* 4 (1937) 529-535.

————. Studies on the control of surra: V. Experiments on surra transmission. *Univ. Phil. Nat. and Appl. Sci. Bull.* 11 (1951) 191-207.

DEL ROSARIO, F. *Dirofilaria immitis* Laidy and its culicine hosts in Manila, I. *Phil. Jour. Sci.* 60 (1936) 45-57.

EYLES, D. E. Studies on *Plasmodium gallinaceum* IV. A comparison of the susceptibility of *Aedes aegypti, Anopheles quadrimaculatus* and *Anopheles freeborni. Am. Jour. Hyg.* 56 (1952) 71-77.

HALL, M. C. Arthropods as intermediate hosts of helminths. *Smiths. Misc. Coll.* 81 (1929) 1-77.

HAUGHWOUT, F. G. Note on the occurrence of Sarcocysts in the Philippine carabao (*Bubalus bubalis* Linn.). *Phil. Agric. Rev.* 20 (1927) 243-247.

HAUGHWOUT, F. G. and S. YOUNGBERG. A trypanosome associated with a fatal disease in the carabao. *Phil. Jour. Sci.* 16 (1910) 77-87.

HEGNER, R., F. M. ROOT, D. L. AGUSTINE and C. G. HUFF. Parasitology with special reference to Man and Domesticated animals. D. Appleton-Century Co., Inc., N.Y. xxi + 812.

JOBLING, J. W. and P. J. WOOLLEY. Texas fever in the Philippine Islands and the Far East. *P. I. Bu. Gov't. Lab.*, Manila, No. 14 (1904) 11.

KELSER, R. A. Transmission of surra among animals of the equine species. *Phil. Jour. Sci.* 34 (1927) 115-141.

KLESOR, M. D. The biology of the nematode, *Thelazia rhodesei* Desmarest, 1827. *Dok. Akad. Nawk. SSSR.* 66 (1949) 309-311. Abst. in *Helminth. Abstr.* 18 (1950) 85. *Vet. Bull.* 20 (1950) 595.

MELNIKOV, N. M. Ueber die Jugendzustande der Taenia cucumerina. *Arch. Naturg., Berlin* 35 (1869) 62-70.

MITZMAIN, M. B. The role of *Stomoxys calcitrans* in the transmission of *Trypanosoma evansi. Phil. Jour. Sci.* Sec. B. 7 (1912) 475-519.

————. The mechanical transmission of surra by *Tabanus striatus. Phil. Bur. Agri. Bull.* No. 28 (1913) 3-11.

————. Collected studies on insect transmission of *Trypanosoma evansi. Tres. Dept. U.S.P.H.S., Hyg. Lab., Bull.* No. 94 (1914) 7-39.

MORGAN, B. B. and P. A. HAWKINS. Veterinary Helminthology. Burgess Pub. Co., Minneapolis 15, Minn., U.S.A. Rev. Ed., 1952. ix + 400.

MORGAN, B. B. and P. A. HAWKINS. Veterinary Protozoology. Burgess Pub. Co., Minneapolis 15, Minn. U.S.A. Rev. Ed. 1952. iv + 187.

MUSGRAVE, W. E. Paragonimiasis in the Philippine Islands. *Phil. Jour. Sci.* Sec. B. 2 (1907) 15-65.

MARTINI, E. The development of a piroplasm and Trypanosoma of cattle in artificial media. *Phil. Jour. Sci.*, 4 (1909) 147-169.

PROMMAS, C. and S. DAENGSVANG. Preliminary report of the study on the life cycle of *Gnathostoma spinigerum*. *Jour. Parasit.* 19 (1933) 287-292.

REFUERZO, P. G. Arthropod intermediate hosts of *Acuaria hamulosa* in the Philippines. *Univ. Phil. Nat. and Appl. Sci. Bull.* 7 (1940) 407-414.

REFUERZO, P. G. and E. Y. GARCIA. The crustacean intermediate hosts of *Gnathostoma spinigerum* in the Philippines and its pre- and intra-crustacean developments. *Phil. Jour. Ani. Ind.* 5 (1938) 351-362.

SANDERS, D. A. Manson's eye worm of poultry. *Jour. Am. Vet. Med. Assoc.* 72 (1928) 568-584.

ST. JOHN, J. S. SIMMONS and F. H. K. REYNOLDS. A survey of mongrel dogs of Manila, Philippine Islands, for helminthic and blood protozoan parasites. *Phil. Jour. Sci.* 44 (1931) 309-311.

SELLARDS, H. W. and L. LEIVA. The effect of stasis on the development of amoebic dysentery in the cat. *Phil. Jour. Sci.* 22 (1923) 39-42.

SMITH, A. M. and J. J. KINYOUN. A preliminary note on a parasitic disease of horses. Headquarters Div. Phil. Gen. Ord. No. 390 (1901) 1-5.

TUBANGUI, M. A. *Eimeria bukidnonnensis*, a new coccidium from cattle, and other coccidial parasites of domesticated animals. *Phil. Jour. Sci.* 44 (1931) 253-271.

————. Worm parasites of Philippine chicken. *Phil. Agric. Rev.* 19 (1926) 3-40.

————. A summary of the parasitic worms reported from the Philippines. *Phil. Jour. Sci.* 76 (1947) 225-322.

————. Preliminary notes on the crustacean vector of mammalian lung fluke (Paragonimus) in the Philippines. *Jour. Parasit.* 32 (1946) 150-151.

TUBANGUI, M. A., B. D. CABRERA and M. G. YOGORE. Studies on the life cycle of the human lung fluke (Paragonimus) in the Philippines, a preliminary report. *Acta Medica Philippina* 6 (1950) 371-372.

WALKER, E. L. Experimental balantidiosis. *Phil. Jour. Sci.* 8 (1913) 333-349.

WENYON, C. M. Protozoology. xvi + 778. 336 figs. (1926) New York, William Wood and Company.

WHARTON, L. D. The intestinal worms of dogs in the Philippine Islands. *Jour. Parasit.* 4 (1917) 80-82.

YUTUC, L. M. Observations on the prevalence of Tabanid flies and surra transmission experiments. *Phil. Jour. Sci.* 78 (1950) 379-387.

————. Observations on Manson's tapeworm, *Diphyllobothrium erinacei* Rudolphi, 1819, in the Philippines. *Phil. Jour. Sci.* 80 (1951) 33-51.

————. *Physaloptera pseudopraeputials* n. sp.—a stomach worm of the cat (Nematoda: Physalopterinae). *Phil. Jour. Sci.* 82 (1953) 221-226.

TABLE I

ARTHROPOD-BORNE PROTOZOA OF DOMESTIC ANIMALS IN THE ISLANDS *

SPECIES	VECTOR OR INTERMEDIATE HOST	HOST	REFERENCE
Trypanosoma evansi (Steele, 1885)	Horsefly (*Tabanus striatus*, *T. reducens*); mosquito (*Aedes aegypti*)	Horse, cattle, dog, carabao, etc.	Smith and Kinyoun, 1901; Mitzmain, 1913; Kelser, 1927; Yutuc, 1950.
Trypanosoma theileri Laveran, 1902	Biting flies (*Tabanus taeniola*); flies of the genus Hippobosca.	Cattle	Martini, 1909; Haughwout and Youngberg, 1920; Morgan and Hawkins, 1952.
Haemaproteus columbae Kruse, 1890	Louse fly (*Pseudolynchia maura*)	Domestic pigeon	Coronel, 1937; Morgan and Hawkins, 1952.
Plasmodium gallinaceum Brumpt, 1935	Mosquitoes of the genera Culex, Anopheles, Aedes, etc.)	Domestic chicken	Africa, Dy and Soriano, 1940; Morgan and Hawkins, 1952; Eyles, 1952.
Bebesia bigemina (Smith and Kilbourne, 1893)	Ticks (*Boophilus annulatus*)	Cattle	Jobling and Woolley, 1904; Martini, 1909; Morgan and Hawkins, 1952.
Bebesia canis (Piana and Galli-Valerio, 1805)	Ticks (*Rhiphicephalus sanguineous*)	Dog	St. John, Simmons and Reynolds, 1931.
Anaplasma marginale Theiler, 1910	Various species of ticks, horseflies, stablefly and mosquitoes.	Cattle	Boynton, 1917; Morgan and Hawkins, 1952.

* Other protozoans listed but not arthropod-borne are: *Entamoeba histolytica*, *Histomonas meleagris*, *Isospora felis*, *I. rivolta*, *Eimeria canis*, *E. tenella*, *E. debliecki*, *E. faurei*, *E. bovis*, *E. bukidnonnensis*, *E. zurnii*, *Balantidium coli* and *Sarcocystis* sp.

ILLUSTRATIONS

(Abbreviations used: as—anterior sucker; vs—ventral sucker; vit—vitellaria; pap—papilla; lp—lip; h.b.—head bulb; ut—uterus; gp.—genital pore; t—testis; ov—ovary; up—uterine pore; nr—nerve ring; oes—oesophagus; vul—vulva; sp—spicule; cl—cloaca; cb—cuticular band; c. pap—cervical papilla; int—intestine; al—caudal wing; b—body.)

PLATE I

Fig. 1.—*Trypanosoma evansi* (Steel, 1885). From Yutuc, 1938.
2.—*Tabanus striatus*. From Yutuc, 1949.
3.—*Tabanus reducens*. From Yutuc, 1949.
4.—*Trypanosoma evansi*. From Kelser, 1927.
5.—*Bebesia canis* (Piana and Gali-Valera, 1895). After Schuberg and Reichenow, 1912 from Wenyon, 1926.
6.—*Riphicephalus sanguineus*, female; enlarged two times.

PLATE II

Fig. 7.—*Paragonimus westermanii*, ova. From Musgrave, 1907.
8.—*Parathelphusa mistio;* first left anterior leg missing; slightly enlarged from the original specimen.
9.—*Paragonimus westermanii* (Kerbert, 1878) Baun, 1899. From Musgrave, 1907. Reduced to one half the original.

PLATE III

Fig. 10.—*Diphyllobothrium erinacei*, procercoid. From Yutuc. 1951.
11.—*D. erinacei, scolex*. From Yutuc, 1951.
12.—*D. erinacei*, three terminal segments. From Yutuc, 1951.
13.—A cyclop, *Cyclops serratus*.
14.—*D. erinacei*, ova. From Yutuc, 1951.
15.—*Gnathostoma spinigerum*, anterior end, male.
16.—*Gnathostoma spinigerum*, caudal end, male.
17.—*Gnathostoma spinigerum*, ova.
18.—*Gnathostoma spinigerum, larva*. From Refuerzo, 1938. (Reduced to one fourth the original.)

PLATE IV

Fig. 19.—*Cheilospirura hamulosa*, ova. From Tubangui, 1926.
20.—*Cheilospirura hamulosa*, larva. From Refuerzo, 1940.
21.—Grasshoppers, *Aeolopus tamulus* and *Oxya sinensis*. From Refuerzo, 1940.
22.—*Cheilospirura hamulosa*, anterior end of the body. From Tubangui, 1926.
23.—*Cheilospirura hamulosa*, posterior end, made. From Tubangui, 1926.

PLATE V

Fig. 24.—*Dirofilaria immitis*, microfilaria.
25.—*Dirofilaria immitis*, anterior end, female.
26.—*Dirofilaria immitis*, caudal end, male.
27.—A mosquito, *Culex quinquefasciatus*. Free hand drawing, about 5×.

PLATE VI

Fig. 28.—*Dispharynx nasuta*, anterior end. From Tubangui, 1926.
29.—*Dispharynx nasuta*, ova. From Tubangui, 1926.
30.—*Dispharynx nasuta*, posterior end, male. From Tubangui, 1926.
31.—Pill bug, *Armadillium* sp. 4x; ventral and dorsal views.
32.—*Tetrameres fissispina*, female. From Tubangui, 1926.
33.—*Tetrameres fissispina*, male. From Tubangui, 1926.
34.—*Tetrameres fissispina*, ova. From Tubangui, 1926.

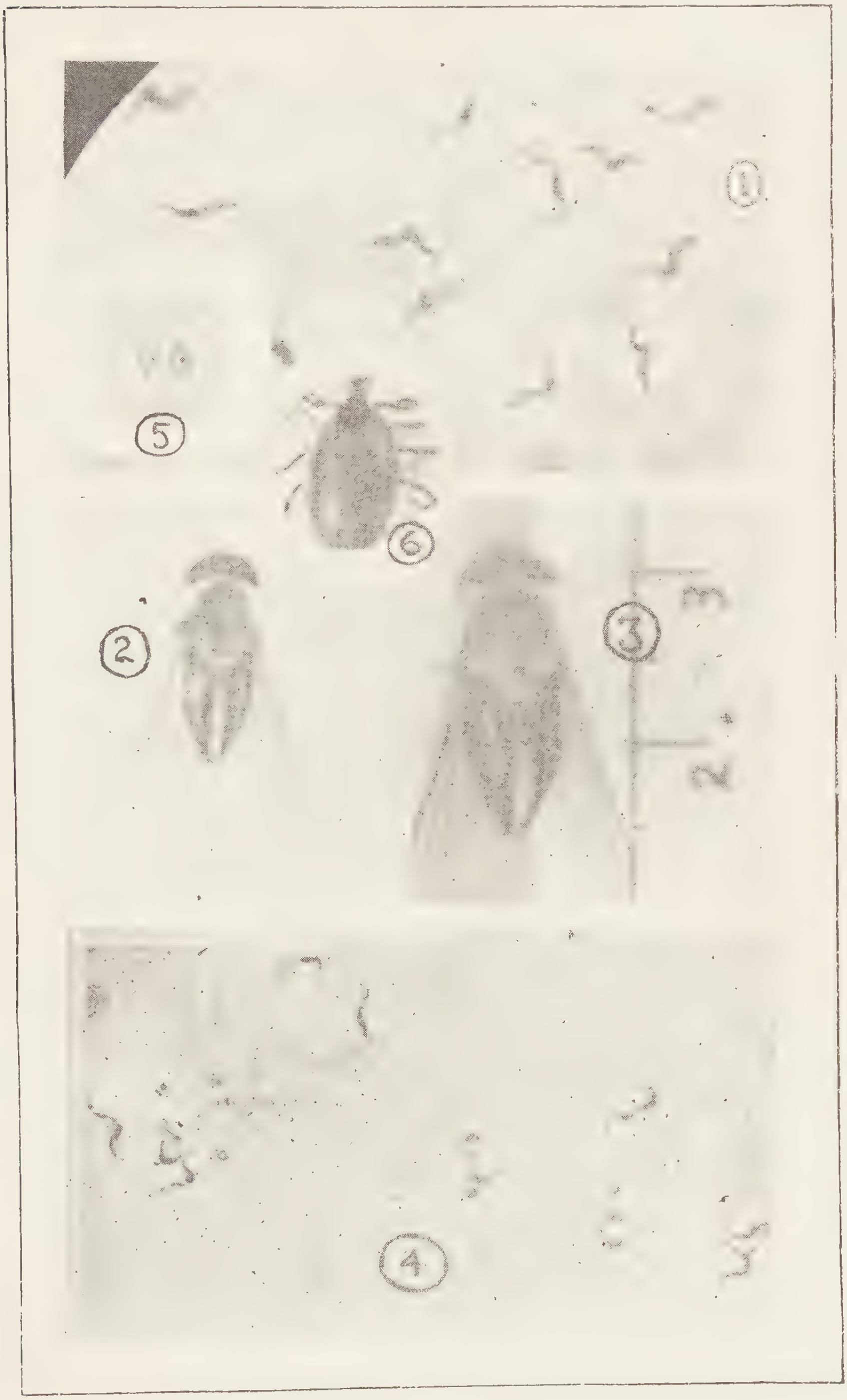
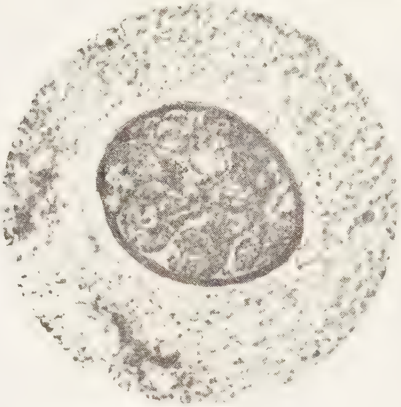
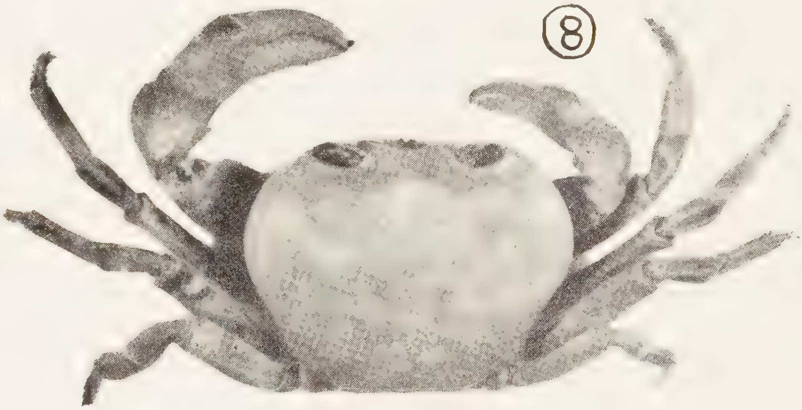


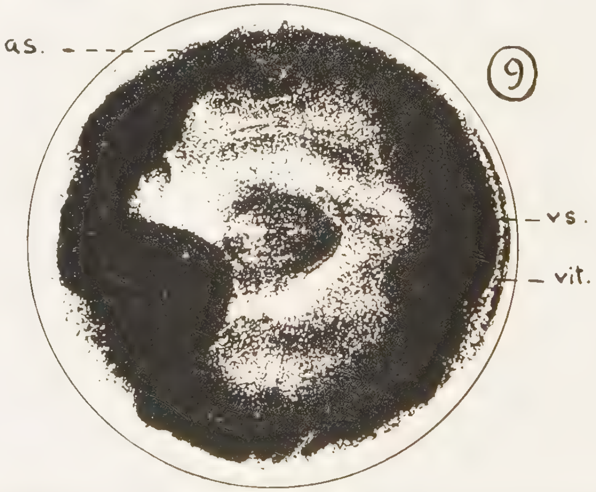
PLATE I



⑦



⑧



⑨

PLATE II

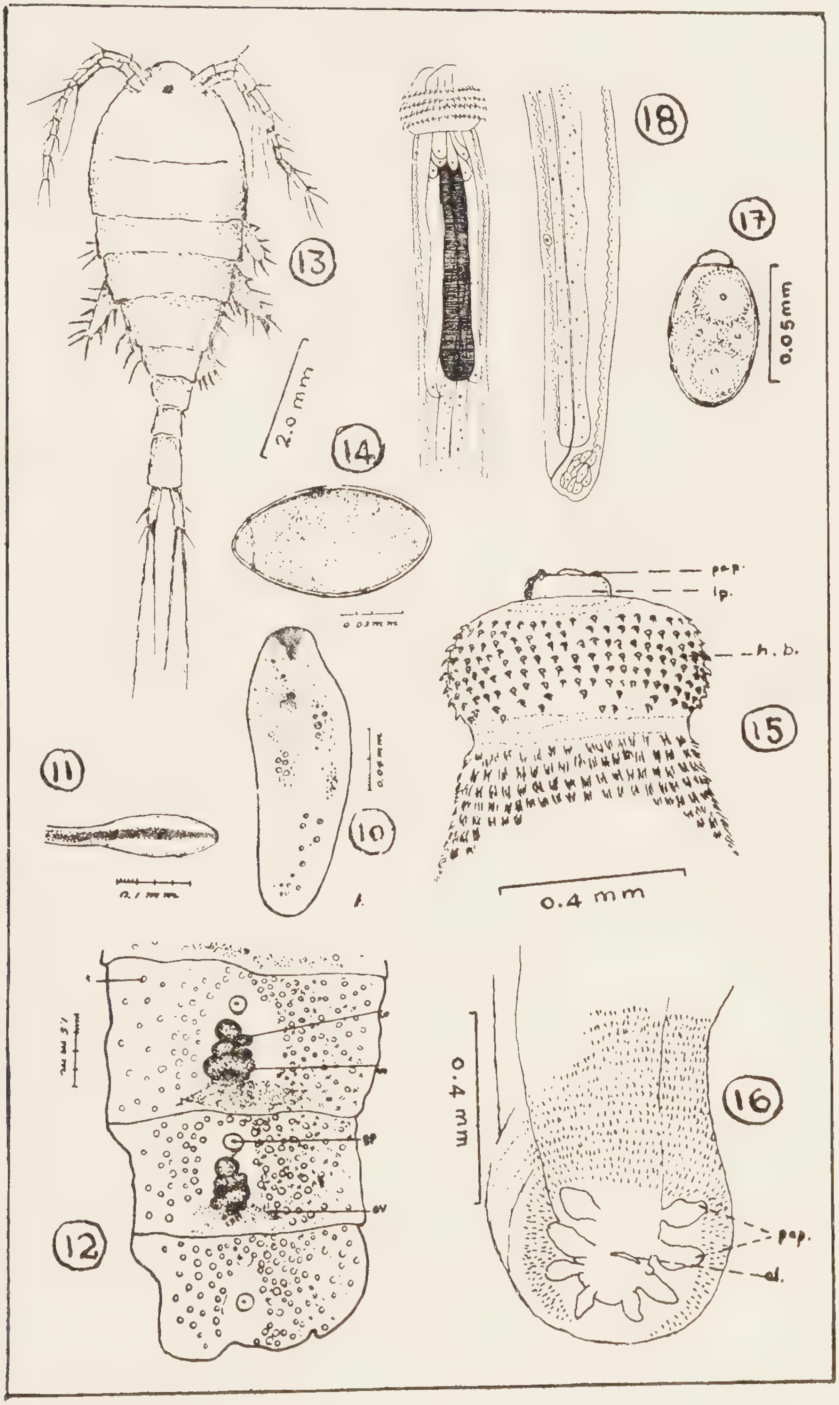

13
2.0 mm
18
17
0.05mm
14
0.03 mm
pap.
lp.
h. b.
15
0.04 mm
11
0.1 mm
10
0.4 mm
12
1.5 mm
sp
ov
0.4 mm
16
pap.
al.

PLATE III

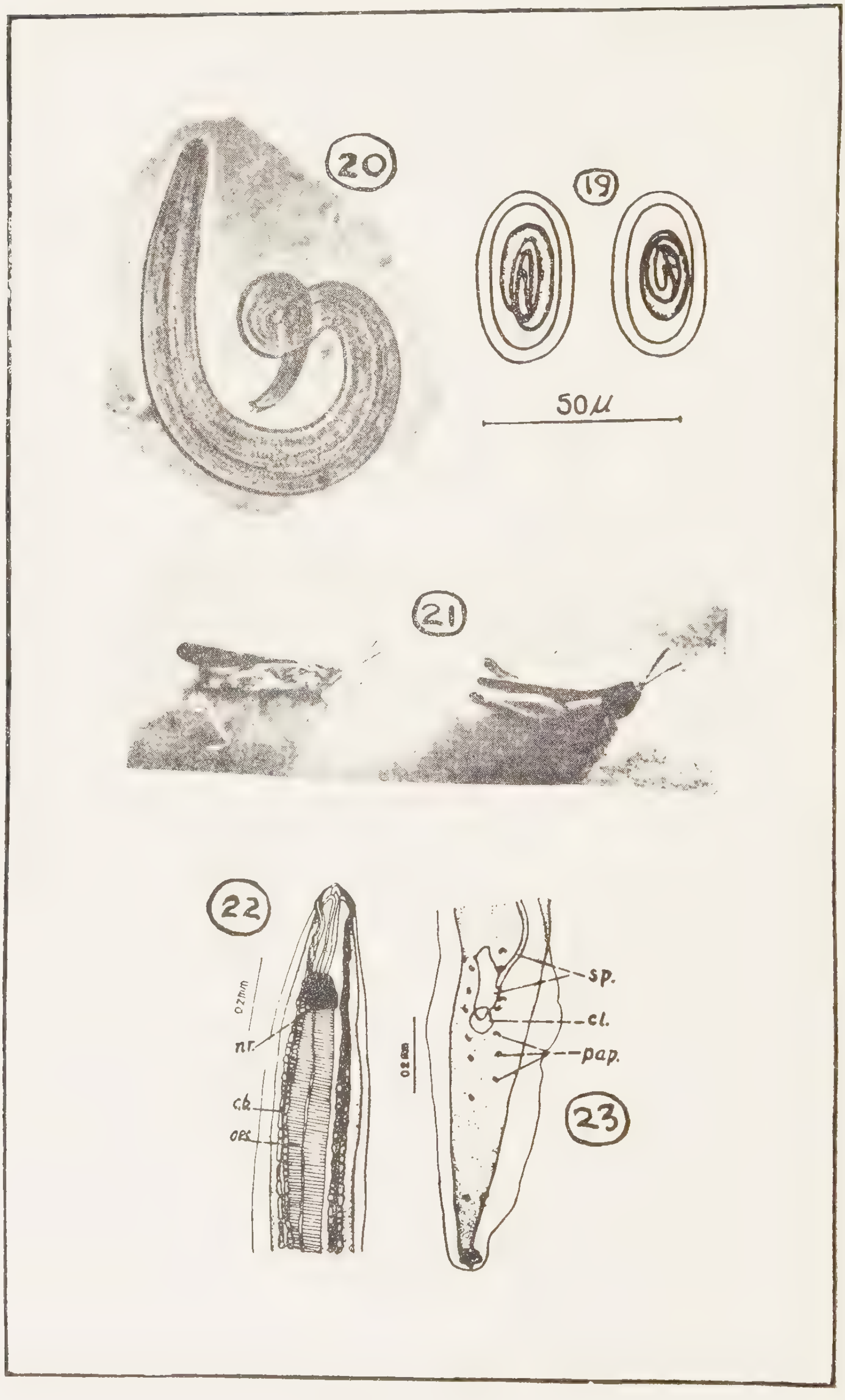

20
19
50μ
21
22
0.2mm
nr.
cb.
oes.
23
sp.
cl.
pap.
0.2mm

PLATE IV

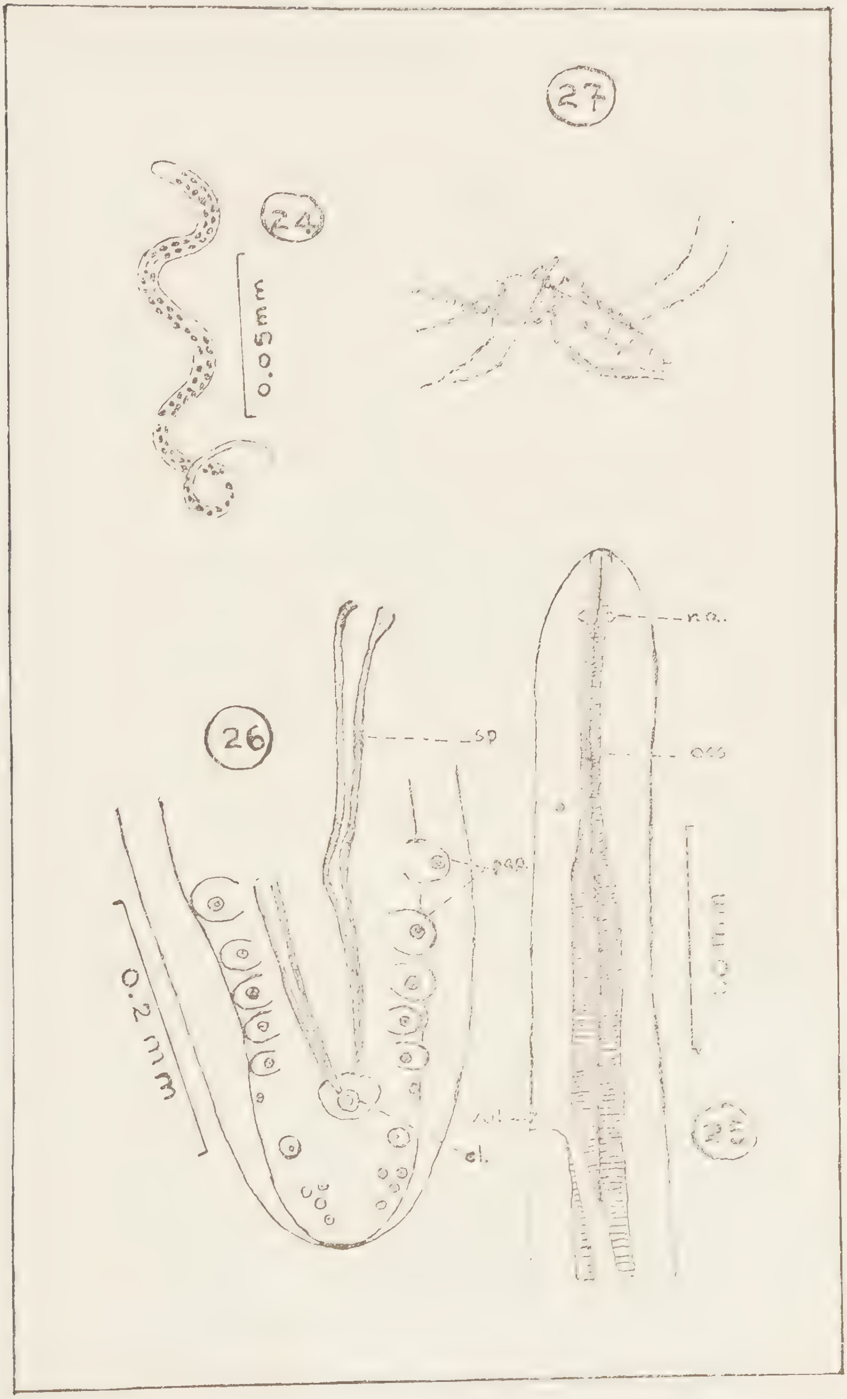
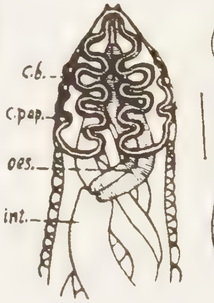
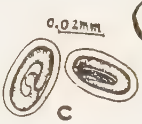

27
24
0.05mm
26
sp
pap.
0.2 mm
cl.
n.a.
oes
vul
25

PLATE V

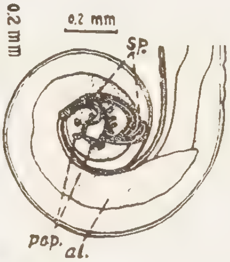
28


c.b.
c.pap.
oes.
int.
0.2 mm

29

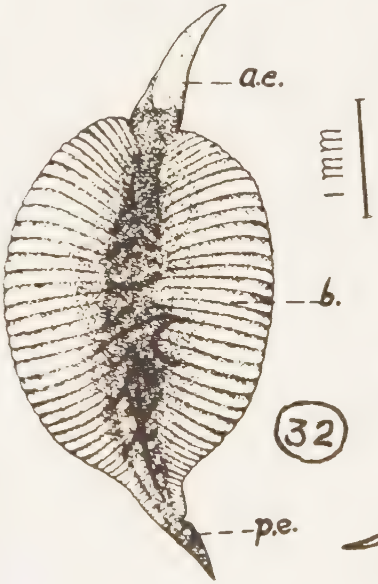


30


0.2 mm
sp.
pap.
al.

31

32



33

34

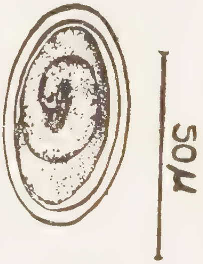


PLATE VI

THE INSECT FAUNA OF THE RYUKYU ISLANDS

By J. Linsley Gressitt
Bishop Museum, Honolulu, Hawaii

The Ryukyu (Riukiu, Loo-choo, Liukiu, Luchu, or Nansei) Islands constitute an archipelago stretching from the southern limits of Japan southwestward to a point east of the northcentral portion of Taiwan. The range of latitude is from about 24° to 29° North. The islands represent a considerably submerged portion of the largely volcanic island chains fringing the continental shelf of Asia. The island groups, from north to south, are Amami, Okinawa, Miyako and Yaeyama, with Miyako and Yaeyama together forming the Sakishima group.

Geologically, the islands are arranged in two curves not far apart. The inner curve is very incomplete, and consists only of the small Tokara group (north of the Amami group), Kume Island (west of Okinawa), and some very small islets just northeast of Taiwan. The outer curve includes the remainder and thus all the large islands. This chain is the remnant of the old Ryukyu cordillera, containing many old rocks, some as ancient as Proterozoic. Much of the land is of Tertiary igneous origin, and some, such as Miyako, consists of raised coral limestone. According to Yabe & Aoki (1923) and Hanzawa (1935), the Ryukyu cordillerra arose in late Permian or early Mesozoic. During the Mesozoic it probably broke into mountain masses by erosion and faulting. Since the Eocene there have been great fluctuations in sea level as a result of crust movements, and three stages when the Ryukyus had a direct land connection with Asia through Taiwan (Oligocene, late Pliocene, early Pleistocene).

The islands were inundated from upper Eocene through lower Oligocene, but only the Yaeyama group was submerged. In the later Oligocene the land rose, but was submerged again between Oligocene and Pliocene, with only the highest points of Amami, Tokuno, Okinoerabu, Okinawa, Ishigaki ang Iriomote remaining above sea level. In the mid-Pliocene volcanic activity broke out, the Tokara group originated, and the sea bottom was elevated 700 meters. In the late Pliocene the Ryukyus consisted of a peninsula from Taiwan and was separated by just over 100 km. from the continent at the middle of the peninsula. At the end of the Pliocene submergence left only the tops of Takara, Kotakara, Amami, Tokuno, Okinoerabu, Iheya, Kume, Tokashiki, Ishigaki and Iriomote above sea level. In earliest Pleistocene the land rose until all the islands of each group were united. Hanzawa states that also the Amami and Okinawa groups were joined and also the Miyako and Yaeyama groups, but Inger (1947) questions this. In early mid-Pleistocene another sinking submerged the islands as much as the Pliocene submergence. Following another emergence about as extensive as at the beginning of the period, the sea level has not shifted more than 20 meters. Thus Miyako and several of the lesser islands have been completely submerged as late as early mid-Pleistocene. This is distinctly reflected in the fauna.

The groups of islands are separated by depressions from 400 to 2000 meters deep. The Tokara strait, just north of Amami, is the deepest, 2000 meters, and coincides with the biogeographical boundary known as Watase's Line separating the Ryukyus and the Oriental Region from Yakushima, Tanegashima, and Japan. The depths of the other straits are: 800 meters between Amami and Okinawa, 1000 meters between Okinawa and Miyako, 400 meters between Miyako and Yaeyama, and 800 meters between Yaeyama and Taiwan. The relative depths very much suggest the faunal relationships.

The climate of the Ryukyus is subtropical and similar to that of northern Taiwan. The average minimum temperature is 57.2°F. (14°C.) in Amami and 59.9°F. (15.5°C.) in Okinawa, and the average maximum temperature is 81°F. (27.2°C.) in Amami and 82°F. (27.8°C.) in Okinawa. Rainfall averages 126.5 in. (3213 mm.) in Amami, 83.3 in. (2115 mm.) in Okinawa and 109.3 in. (2776 mm.) in Iriomote.

According to Wilson (1920) the ligneous flora consists of a littoral fringe of wide-spread subtropical plants, and many endemics, mostly evergreen, in the mountains. Three dominant elements are the mangrove, *Pinus luchuensis* and *Cycas revoluta*. Of 351 species of woody plants, 71 are endemic. The Tokara strait is a significant boundary, as with the fauna, in spite of species in common between Amami-Oshima and Japan. The distribution of the Ryukyu plants is tabulated by Masamune (1934).

Faunistically, the Ryukyus belong essentially to the Indo-Chinese Subregion of the Oriental Region, but have some Palearctic and Philippine affinities. Though many species are possessed in common with Japan, quite a few of these belong to Oriental genera which reach the warmer parts of Japan. Consistent with the fact that the islands are continental, the fauna is well rounded in that most important families of east Asian insects are represented. However, the number of species in a given spot may not be very great and the fauna is apparently depauperized compared with Japan or Taiwan as a result of submersion, reduction in the size of the islands and loss of vegetation.

As an example of faunal relationships may be taken the Cerambycidae (longicorn beetles), reported upon by myself (Gressitt, 1951). The fauna appears to consist of 52 Oriental, 10 Palearctic, and 26 endemic species. Of the 26 endemics, 25 appear to have Oriental affinity, and only 1 to be Palearctic in relationship. Of the 52 non-endemic species of Oriental relationship, 43 occur in Taiwan, 1 in Hainan but not in Taiwan, and 8 occur also in Japan, or Japan and North China, but belong to Oriental genera. Of the 43 species occurring also in Taiwan, 12 are found in South China as well, 3 in Taiwan and Botel-Tobago (of which 2 are included in 3 in Formosa and the Philippines), and 4 additional are widely distributed Oriental species. Of the total, 31 Ryukyu species occur also in Japan, 19 in China, and 16 are found from Japan to Taiwan. The Philippine element is not conspicuous in this family. However, in addition to the 3 species found also in the Philippines, 1 of the genera concerned is primarily Philippine in constituency, though also having a species recorded from the Asiatic mainland. The genus *Iphrobrium* is known from Okinawa, Iriomote and many Pacific islands, including Melanesia and the Philippines, but not Formosa.

In the weevils there is a conspicuous Philippine relationship in *Pachyrrynchus infernalis* Fairmaire which is found on the Yaeyama Islands. The tribe Pachyrrynchini is almost entirely Philippine in its makeup, but includes five species on Botel-Tobago Island, just east of southern Formosa, but none on Formosa or the Asiatic mainland.

In the butterflies there is another Philippine representative, the large danaid *Hestia leuconoe*. This species is also found along the southeast coast of Taiwan, where several Philippine elements are found which do not occur in other parts of the island.

In some other groups of insects, such as the Chrysomelidae (Chujo, 1935), the relationships are more or less as indicated above, except that the collections were more extensive from the southern islands. One author (Kubo) considered that only Okinawa and Sakishima groups belonged to the Oriental Region, based on the fresh-water shrimps.

In the amphibians Inger (1947) states that the fauna consists of five Oriental species and nine endemic forms, with the only Palearctic species apparently an introduction. Only one of the endemic species belongs to an Holarctic genus. In the Osumi group (Yakushima and Tanegashima) there are five Palearctic species, none of which occur south of the Tokara Strait—that is, in the Ryukyu chain itself. Mammals are poorly represented, but in Amami there is a peculiar endemic rabbit. Yamashina (1941) states that the three endemic Ryukyu birds are Palearctic in relationship.

To compare the relationships between the island groups, data is presented in the following table on the Cerambycidae:

NUMBERS OF SPECIES

	TOTAL	ENDEMIC	IN COMMON WITH							
			JAPAN	AMAMI	OKINAWA	MIYAKO	ISHIGAKI	IRIOMOTE	TAIWAN	CHINA
Amami	45	6	23	—	25	4	13	15	24	18
Okinawa	51	5	23	25	—	6	16	21	31	21
Miyako	8	0	3	4	6	—	6	6	3	2
Ishigaki	29	2	7	13	16	6	—	19	19	13
Iriomote	34	2	9	15	21	6	19	—	21	10

Of those endemics restricted to more than one island within the Ryukyus, one is common to Amami and Okinawa, one to Okinawa and Miyako, four to Okinawa and Sakishima, two to the Yaeyama group, and two common to all the main groups. Only one species is restricted to the Ryukyus and Yakushima. As one might expect, the affinities of the Amami fauna are closer to Japan than are those of the more southern islands, and the Yaeyama group possesses a higher proportion of species in common with Taiwan than do the other island groups. Amami and Okinawa have many species in common, quite a number of which do not extend further southward.

As to richness, the Amami group and Okinawa vie for the maximum number of species for one island group. In most groups of insects Okinawa has been more thoroughly collected than has Amami. Miyako is the poorest of the major islands. Possibly many of the species on Miyako have been introduced by man. Ishigaki and Iriomote are similar in faunal representation, but Iriomote may be richer, partly because it has more natural vegetation remaining. The Yaeyama group, though poorer than Okinawa or Amami, possesses a number of forms not found in the northern groups.

The Daito Islands, some distance southeast of the Ryukyus, have a small insect fauna consisting largely of widespread forms (Yashiro, 1939), and thus are typical of an isolated low oceanic island, possibly lacking in endemics.

The insect fauna of the Ryukyus is still not well known and much collected material has not yet been studied. Among early insect collectors in the Ryukyus were B. J. Ferrié and J. E. A. Lewis. One of the larger early collections was made by Dr. J. C. Thompson (Victor Kühne) for the California Academy of Sciences in 1911. Over a period of years collections were accumulated by Japanese entomologists, particularly at Sapporo, Fukuoka and Taihoku (Taipeh). Among those who collected and reported upon insects during this period were S. Matsumura, T. Shiraki, T. Esaki, R. Takahashi, S. Issiki, Y. Okada (1938), T. Okada (1939), S. Kuwana, Y. Miwa (1935), S. Asahina, A. Umeno and others. In 1932 and 1934 I collected on the five principal islands, and much of this material is at the California Academy of Sciences. In 1945 a number of Americans, including R. M. Bohart (Bohart and Ingram, 1946), G. E. Bohart, F. W. Werner, myself and others collected on Okinawa, and this material is largely at the U.S. National Museum, Museum of Comparative Zoology, and California Academy of Sciences. During the past few years the Pacific Science Board has been sending entomologists to the Ryukyus, among them R. M. Bohart (1951), G. E. Bohart (1953), F. Werner (1952), and T. Shiraki. The resulting collections are largely at the Bishop Museum, and in Tokyo. Since the war several papers have been published by Americans on Ryukyu insects.

The economic insects of the Ryukyus have not been adequately studied. On some islands the sweet potato is the most important crop and the sweet potato weevil, *Cylas formicarius,* is a major pest. The West Indian sweet potato weevil, *Eucepes postfasciatus,* is also a pest on Okinawa. Other sweet potato insects include a crown boring pyralid, *Omphisia* sp., aphids and others. Pests of rice include rice borers (*Chilo simplex*); of sugar cane a white fly (*Aleurodes bergi*) and a mealybug (*Trionymus sacchari*); of pineapple a mealybug (*Pseudococcus* sp.); and of citrus a longicorn beetle (*Anoplophora macularia*). Malaria, filariasis, and Japanese "B" encephalitis are carried by mosquitoes in the Ryukyus and a filarial eye disease in horses on Ishigaki is carried by *Musca conducens* (G. Bohart, 1953).

LITERATURE CITED

BOHART, G. E. 1953. Report on entomological investigations. Scientific Investigations in the Ryukyu Islands (SIRI). Pacific Science Board, National Research Council, Washington. 20 pp. mimeo.

BOHART, R. M. 1951. A survey of insects of medical importance on Ishigaki and Iriomote Islands, southern Ryukyus. Pacific Science Board, National Research Council, Washington. 16 pages, tables and maps, mimeo.

BOHART, R. M. and R. L. INGRAM. 1946. Mosquitoes of Okinawa and islands in the central Pacific. Navmed 1055, Bur. Med. and Surgery, Washington. 110 pp.

CHUJO, M. 1935. Chrysomelidae of Loo-choo Archipelago (II). *Trans. Nat. Hist. Soc. Formosa,* 25: 203-211.

GRESSITT, J. L. 1951. Longicorn beetles from the Ryukyu Islands (Coleoptera: Cerambycidae). *Philippine Journal of Science,* 79: 193-235, 5 figs. including map.

HANZAWA, S. 1935. Topography and geology of the Riukiu Islands. Tohoku Imp. Univ. Sci. Rept. (2) *Geology*, 18: 1-61, pls., maps.

INGER, R. F. 1947. Preliminary survey of the amphibians of the Riukiu Islands. Fieldiana: *Zoology*, 32: 297-352, 4 maps, 2 figs.

KUBO, I. 1941. On some fresh-water shrimps from the Ryukyu Islands. *Biogeographica*, Tokyo, 3: 303-318, 7 figs., 1 pl.

MASAMUNE, G. 1934. On the phytogeography of the Ryukyu Archipelago. *Bull. Biogeog. Soc. Japan*, 5: 29-86.

MIWA, Y. 1935. Coleoptera from Amami-Islands in Loo-choo Archipelago. *Trans. Kansai Ent. Soc.*, 6: 11-30, 2 pls.

OKADA, T. 1941. Dipteran Insects of Ryukyu Islands. *Biogeographica*, Tokyo, 3: 249-272, 5 figs.

OKADA, Y. 1938. The outline of the Okinawa Islands. *Biogeographica*, Tokyo, 3: 1-64, 38 figs., 1 map.

WERNER, F. 1952. Progress report on entomological investigations. Scientific Investigations in the Ryukyu Islands (SIRI). Pacific Science Board. National Research Council, Washington. 22 pp. mimeo.

WILSON, E. H. 1920. The Liukiu Islands and their ligneous vegetation. *Journal Arnold Arb.*, 1: 171-186.

YABE, H. and R. AOKI. 1923. A summary of the stratigraphical and paleontological studies of the Cenozoic of Japan. *Proc. Pan-Pacific Sci. Congr.* (Australia), 1: 954-969.

YAMASHINA, MARQUIS Y. 1941. On the three endemic birds in the Ryukyu Islands—their classificatory position and zeogeographical meaning. *Biogeographica*, Tokyo, 3: 319-328 (English resumé).

YASHIRO, H. 1939. Insects of Minami-Daito Island (Loo-choo). *Biogeographica*, Tokyo, 3: 127-130, 3 figs.

HISPINE BEETLES OF THE COCONUT PALM

By J. Linsley Gressitt
Bishop Museum, Honolulu, Hawaii

The hispine beetles or hispids represent a specialized subfamily of the Chrysomelidae or leaf beetles. There are about 2500 known species, most of which are tropical. The majority of the species measure from 5 to 25 millimeters in length and are narrow, or flat and broad, or armed with long spines.

More than one-quarter of the hispids of known host relationships attack palms. A similar number attack members of the grass family, and include important pests of rice, sugar-cane, maize, sorghum, bamboos and other grasses. Others feed in Pandanus, *Freycinetia,* orchids, members of the ginger family, as well as other groups of plants, primarily monocotyledons, but including some dicotyledons. Most of the palm-feeding species are slender, spineless types, whereas many of those feeding in rice, sugar cane, bamboo and grasses are small and spiny. These beetles are moderately host-specific, but sometimes several plant families are attacked by members of the same genus.

This group is of great economic importance, in many places including pests of coconut palms second only to the rhinoceros beetle or palm weevil, and sometimes the most serious pest where those larger beetles do not occur.

Of those feeding upon palms, 20 genera, and over 50 species, are represented. Five of these are limited to the tropical New World, 3 to Africa and 2 to the Seychelles. Ten genera attack palms in Asia and the Pacific islands, and of these, 2 are restricted to Asia, 4 to Oceania, 3 are in common between Asia and Oceania, and 1 is in common between Madagascar and Oceania. Of the 5 Neotropical genera, 4 probably attack the coconut palm, as well as other palms. Of the 15 Old World genera, species of 10 feed upon the coconut palm and members of 13 attack other palms. These statistics are a little puzzling when considering that the coconut palm is thought to be Neotropical in origin, and also that this subfamily is most richly represented in the Neotropical Region. Probably less attention has been paid to them in the Neotropics.

The typical habit of the members of the subfamily Hispinae is as leaf-miners. However, many of those feeding upon palms live between the leaves as they begin to open at the top of the crown of the palm. Both larvae and adults as a rule feed upon the upper surfaces and the parenchyma of the leaflets, lying between the upper surfaces of the leaflets which are still folded together before the new fronds open out. The result of this feeding is the elimination of large areas of tissue, forming splotches, sometimes more or less continuous, which wither as the frond opens out. When the beetles are abundant the new fronds may be largely shrunken and withered, and death to the palm may result.

These beetles are essentially sun-loving insects. When palms are scattered in shady jungle in the natural condition, the beetles rarely become abundant, and are generally unnoticed. However, when palms are cultivated in large solid stands without shade over the palms, as in most coconut groves, the situation becomes ideal for hispids, with maximum exposure to sunlight and unlimited food, so that very large populations may result. In dry weather the beetles breed more rapidly, and in periods of drought or after volcanic eruptions may become very dangerous. On various occasions very severe damage has resulted, as with cases in New Britain under the German regime at the beginning of this century, when mile-wide plantings of young palms, numbering 50,000 plants were destroyed in a short time, and in more recent cases in Fiji, Saipan and elsewhere. In such circumstances the biological equilibrium has been greatly upset, natural enemies have been favored much less than the hispids, or the beetles have spread without their parasites.

Not long before World War II one species, *Brontispa mariana* Spaeth, had been introduced from the Carolines to Saipan and then to other islands in the Marianas and very severe damage, to the point of near extermination of coconut palms on Saipan, resulted. During the winter of 1947–48 Dr. W. H. Lange (1950) was sent by the Pacific Science Board to the Philippines, Malaya and Java to search for parasites. He returned to Saipan with two species, *Haeckeliania brontispae* Ferriere and *Tetrastichus brontispae* (Ferriere). The former, an egg parasite, did not become established, but the *Tetrastichus* has proved effective in control (Doutt, 1950). In the native home of this *Brontispa,* Yap and other islands of the central and western Carolines, no parasite is known, yet the beetles are rarely of any importance in the coconut groves, though not known to atttack other palms for certain. However, an earwig, *Chelisoches morio* (Linn.), is commonly found feeding on the beetle larvae.

Another Micronesian species of *Brontispa* [*B. chalybeipennis* (Zacher), synonym; *namorikia* Maulik], is found in the eastern Carolines and in the Marshall Islands. It has only been recorded from the coconut palm, and no parasites are known, but it has rarely caused very serious damage to coconut groves. Obviously further study of it is necessary. On Ponape I found a dead adult in the axil of a *Pandanus* plant under native *Exhorhiza* and *Ponapea* palms. As there were no coconut palms in the neighborhood, it seems likely that the beetle may have been feeding on one of the native palms. A third Micronesian species, *Brontispa palauensis* (Esaki and Chujo) (*yoshinoi* Barber), is restricted to the Palau islands. It also seems to cause rather little damage, though no parasites of it are known (Hagen and Doutt, 1950). In some cases palms killed by *Oryctes rhinoceros* undoubtedly had their deaths hastened by attack by this *Brontispa,* but the percentage of Oryctes-damaged palms also attacked by the *Brontispa* appeared to be rather low, though the latter was abundant when found in a particular palm (Gressitt, 1953).

In New Guinea, *Brontispa longissima* (Gestro) (*froggatti*) is an important pest, though generally less serious than *Promecotheca papuana.* In addition to the coconut palm it attacks the betel palm, sago palm and some introduced palms. The period from egg to adult takes 6 to 7 weeks and adults may live 200 to 220 days. The parasites *Thricogrammatoidea nana* Zehn. and *Achrysocharis* sp. are known, and control by "Black leaf 40" or lead arsenate spray was recommended by Froggatt and O'Connor (1941). Several other species of *Brontispa* are of importance, damaging coconut palms, or of potential importance. They occur in New Guinea, Java, the Philippines, Mauritius and Rodriguez (Maulik, 1938).

The genus *Promecotheca* contains several species of considerable importance. These species are leaf-miners, both in new and older coconut leaves. *Promecotheca reichei* Baly some years ago was of the greatest importance in Fiji. After the parasite *Pleurotropis parvulus* Ferr. was introduced from Java, this hispid was very greatly reduced. In Fiji the pest is no longer a problem and Mr. O'Connor was unable to find any to show Mr. Owen and myself on our visit in 1952. This phenomenal success was the subject of the book entitled, "The biological control of an insect in Fiji," by T. H. C. Tayler (1937). In the Wallis Islands this species is reported (Cohic, 1950) not to be very serious. There is an indigenous parasite, *Oligosita utilis* Kow., but the Javan *Pleurotropis* has not been introduced. In Samoa and Tonga the species is also not of great importance. It may be native in Samoa, Tonga and Wallis, and introduced to Fiji. Another species (*P. bicolor*) from Fiji, is known only from a native palm.

Another species of *Promecotheca, P. papuana* Csiki (*antiqua* Weise), is one of the more serious pests of coconut in New Guinea and neighboring islands, particularly on Manus Island. The beetle attacks palms of any age, and is more serious where palms are unhealthy or injured. The beetle's native hosts are apparently the sago palm and nipa palm, from which it can re-infect coconut groves. The oil palm is not attacked. The larvae are true leaf-miners, feeding between the upper and lower surfaces of the leaflets, causing large wilted areas. The life-cycle, from egg to adult, occupies 52 to 63 days. The adult beetles feed on the undersurfaces of the leaflets, parallel to the veins, and live up to 160 days. Three egg parasites, *Closterocerus splendens, Anastatus* sp. and *Telenomus* sp., are known, and two larval parasites, *Eurytoma promecothecae* and *Derostenus* sp. Ants of several species, particularly *Pheidole,* attack eggs or larvae. The red ant *Oecophylla* also attacks *Promecotheca,* but does damage to the host to counteract its usefulness. A pentatomid bug, *Amyota reciprocus,* attacks adult beetles, but is rare. In addition to spraying, control by means of flares of kerosene in half coconut shells on ends of bamboo poles is recommended (O'Connor, 1940; Froggatt and O'Connor, 1941).

Promecotheca cumingi Baly is a species destructive to coconut palms in the Philippines, and also occurs in Borneo and the Malay Peninsula. It is reddish brown, 7.5–10 mm. long. This is also a true leaf-miner, the eggs being laid separately on under sides of the leaflets of young palms. The eggs hatch in two weeks and the larvae mature in one month. Pupation takes place inside the mine in the leaf. The adults feed on young leaflets slitting them longitudinally. Two chalcidoid parasites are known, one of the egg and the other of the larva and pupa.

Promecotheca opacicollis Gestro, of New Hebrides, is a fairly serious pest of coconut. It is also found in the Santa Cruz Islands. *P. nuciferae* Maulik, of Celebes, also feeds on the coconut palm. Some of the other species of the genus in the Solomons, Indonesia and the Philippines, are known to feed on native palms and *Alpinia* but some do not have their hosts recorded. *Promecotheca guadala* Maulik is a pest of coconut in the Santa Cruz group of the Solomons.

The most important hispid pest in western Indonesia is *Plesispa reichei* Chapuis, which has been called the two-colored coconut leaf-beetle. It is an important pest in Malaya, Sumatra and Java. It is 7–8 mm. long and orange and black. The eggs are laid singly in leaves and the larvae feed between the not yet opened leaves, as do the adults. The larval stage lasts from 30 to 40 days, and the adults live from 6 to 9½ months. The beetle is particularly destructive to young coconut palms, and seedlings 2–3 years old are often killed. The royal palm is also attacked. Corbett (1923) recommended that coconut nurseries should be away from coconut groves, that hand killing be practised, as well as spraying with lead arsenate.

Another species of the same genus, *Plesispa nipae* Maulik, is a pest of betel palm, sago palm and nipa palm, and has habits similar to *P. reichei*. *Plesispa cocotis* Maulik is recorded from coconut in New Caledonia, and *P. ruficollis* Spaeth from coconut in New Guinea.

Another Oriental genus of hispids of importance to palms is *Wallaceana* (*Wallacea*). *W. palmarum* (Gestro) feeds on betel palm and nipa palm sometimes killing the former. This is an elongate-oblong beetle about 6 mm. in length. An Indian species of the genus attacks the date palm.

The genus *Aulostyrax* is known only from the Solomons. *A nuciferae* Maulik attacks the coconut palm. It is a broad flat species about 10 mm. long.

In Samoa there is an undescribed genus and species which feeds in native palms. It is related to *Brontispa*. It is possible that it might also attack the coconut palm, particularly under unfavorable circumstances.

The genus *Oxycephala* includes rather large species, some of which are brightly marked with metallic colors. Most of the species feed on the surfaces of very new *Pandanus* leaves before they emerge from the center of the crown. A new species collected in Palau several months ago feeds in the same situation in *Freycinetia,* and another endemic Palauan species feeds in *Flagellaria* and *Pleomela* as well as in *Pandanus,* and rarely *Freycinetia*. A third in Palau is known only from *Pandanus,* but some of these might occasionally attack coconut palms. Two species in New Guinea and one from the Solomons have been recorded from coconut palm.

Xiphispa is a genus of elongate brown species with a long process between the antennae. *X. biroi* Gestro from New Guinea is known to attack the betel palm. A species from Madagascar is recorded from coconut palm.

Botryonopa includes some of the largest Oriental species, many of them an inch long, and mostly brown or reddish. *B. sanguinea* Guerin feeds on opening leaves of coconut and other palms in Java.

The genus *Callispa* contains many species throughout the Orient. They are broadly oval or oblong, and often metallic, or pale in color. Many of the species feed on bamboo, but *C. roepkei* Uhmann and *metroxylonis* Uhmann from Java feed in the sago palm. One Philippine species attacks orchids.

Among other genera of importance are *Estigmena,* feeding in bamboo, *Anisodera* from a wild ginger, *Leptispa* from bamboo, sugar cane and rice, *Choeridiona* from turmeric and *Curcuma, Oncocephala* from orchids and sweet potato, *Downesia* on bamboo, *Agonia* in bamboo and orchids, *Gonophora* in wild ginger and orchids, all in the Orient, and *Pharangispa* on wild ginger in the Solomons.

The preceding are all non-spiny types; and of the spiny groups *Hispellinus* is a leaf-miner in rice and other grasses, *Hispella* in Sorghum and other grasses, *Asamangulia* in sugar cane and rice, *Phidodonta* on sugar cane and wild grass, *Rhadinosa* in sugar cane, maize and rice, *Dactylispa* in rice, grasses, bamboo, *Cinchona* and members of the Rosaceae, *Hispa* in maize, rice, apple and others, and *Platypria* in sugar cane, *Zizyphus jujuba* and *Erythrina.*

SELECTED BIBLIOGRAPHY

COHIC, F. 1950. Les insectes suisibles aux plantes cultivées dans les Wallis et Futuna. *L'Agronomie Tropicale,* 5 (11-12): 563-581.

CORBETT, G. H. 1923. The two-coloured coconut leaf-beetle (*Plesispa reichei* Chap.) *Dept. Agric. S. S. Fed. Malay States Bull.,* 34: 1-20, 3 pls.

DOUTT, R. L. 1950. Field studies on the parasites of *Brontispa mariana* Spaeth. *Proc. Hawaiian Ent. Soc.,* 14: 55-58, 1 fig.

ESAKI, T. 1943. Injurious insects on the inner South Sea Islands. *Shokubutsu oyobi Dobutsu* (Botany and Zoology, theoretical and applied), 11: 269-274, 437-440, 515-521, 587-591, 675-678; figs.

FROGGATT, J. L. 1936. Entomological notes. *New Guinea Agric. Gaz.,* 2 (1): 10-14.

————. 1937. *Promecotheca antiqua* Wse.—Leaf pest of coco-nuts. *New Guinea Agric. Gaz.,* 3 (2): 21-22.

————. 1939. The coconut leaf-miner, *Promecotheca papuana* Csiki (*antiqua* Wse.). *New Guinea Agric. Gaz.,* 5 (1): 3-10.

FROGGATT, J. L. and B. A. O'CONNOR. 1941. Insects associated with the coconut palm. II. *New Guinea Agric. Gaz.,* 7: 125-133.

GRESSITT, J. L. 1950. The hispine beetles of China (Coleoptera: Chrysomelidae). *Lingnan Science Jl.,* 23: 53-142, pls. 4-8.

————. 1953. The coconut rhinoceros beetle (*Oryctes rhinoceros*) with particular reference to the Palau Islands. *Bernice P. Bishop Mus. Bull.,* 212: viii and 157 pp., 50 figs.

HAGEN, K. S. and R. L. DOUTT. 1950. *Brontispa yoshinoi* Barber, a description of adult and immature stages. *Ann. Ent. Soc. Amer.,* 43: 311-319, 17 figs.

LANGE, W. H. 1950. The biology of the Mariana coconut beetle, *Brontispa mariana* Spaeth, on Saipan, and the introduction of parasites from Malaya and Java for its control. *Proc. Hawaiian Ent. Soc.,* 14: 143-162, 4 figs.

MAULIK, S. 1919. The fauna of British India. Chrysomelidae (Hispinae and Cassidinae). London, Taylor & Frances. xi and 439 pp., 139 figs.

————. 1937. Distributional correlation between Hispine beetles and their host-plants. *Proc. R. Zool. Soc. Lond.,* A 1937: 129-159.

MAULIK, S. 1938. On the structure of larvae of hispine beetles V (with a revision of the genus Brontispa Sharp). *Proc. R. Zool. Soc. Lond.*, B 108: 49-71, figs.

O'CONNOR, B. A. 1940. The coco-nut leaf-miner, *Promecotheca papuana* Csiki, and its parasites. *New Guinea Agric. Gaz.*, 6 (2): 20-30.

RISBEC, J. 1935. Note sur les moeurs du Chelisoches morio Fabr. *Bull. Soc. Ent. France,* 40:31-32.

TAYLOR, T. H. C. 1937. The biological control of an insect in Fiji. *Imp. Inst. Ent.*, x and 239 pp.

UHMANN, E. 1952. Austral-asiatische Hispinae des Zoologischen Museums der Humboldt-Universität zu Berlin. 7. Teil: Cryptonychini. 126 Beitrag zur Kenntnis der Hispinae (Chrysom. Coleopt.). *Mitt. Münch. Ent. Ges.*, 42: 71-86, 6 figs.

SOME MIMICRY PATTERNS OF PHILIPPINE INSECTS

By Henry Townes
Bureau of Plant Industry, Manila

Abstract

An active diurnal insect moving across a varied background is conspicuous, no matter what its shape or color. It appears that in such insects protective resemblance is largely absent as a function of form and color, and that mimicking and ruptive appearances have become dominant.

Among the active diurnal insects there is a strong convergence towards certain color patterns. Those that are ruptive or otherwise concealing or confusing in function occur in any part of the world where the conditions of light and shade permit their efficient functioning, while those that are mimicking are centered in certain geographic areas. The series of mimicry patterns dominant in the Philippines is different from that in other parts of the world. As a group they give the Philippine fauna a distinctive gross appearance. Separately, they may be compared with color patterns in other areas to furnish data on the origin and relation of several elements of the Philippine fauna.

PARASITES OF TENT CATERPILLARS (LEPIDOPTERA: LASIOCAMPIDAE) IN THE LOWER FRASER VALLEY OF BRITISH COLUMBIA, CANADA[1]

By J. H. McLeod[2] and G. L. Ayre[2]
Biological Control Section, Entomology Laboratory
University of British Columbia, Vancouver, B.C., Canada

Introduction

There have been five cycles of abundance of *Malacosoma* spp. in British Columbia since 1900 (Baird, 1917; Glendenning, 1923; Twinn, 1938, 1942). In 1950 the first evidence of the most recent cyclical increase in the lower Fraser Valley of British Columbia was obtained. Two species of tent caterpillars were present: *Malacosoma disstria* Hbn. in one focal area of four square miles about 20 miles from the coast and *M. pluviale* (Dyar) in small, localized colonies along the coast. By 1953 the infestation had spread to more than 400 square miles and the two species were widely distributed and intermixed over the area.

During the cycle of abundance of *Malacosoma* spp. that began in 1950, the biological control factors were investigated with particular reference to the parasite species.

Methods and Materials

From 1950 to 1953 representative samples of eggs, larvae, and pupae of *Malacosoma* spp. were collected in the infested area between Vancouver and Chilliwack and were reared in the laboratory. All samples were obtained from ground level to a height of not more than 12 feet.

Egg masses laid in 1950 were collected in September and April; those laid in 1951 and 1952 were collected in April. The number of egg masses per collection ranged from 5 to 153, depending upon their abundance. The eggs in representative masses were counted to obtain the average number per mass of each species. Each egg mass was removed from the twig on which it had been deposited and was placed in a 90-by-20-mm. glass vial with a strip of white blotting paper to which moisture was applied with a medicine dropper. The vials were tightly stoppered with cotton batting. When parasite emergence started, the parasites were removed daily with an aspirator and the number and species were recorded.

---

[1] Contribution No. 3167, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

[2] Agricultural Research Officer.

Collections of larvae included all instars and because larval development was not uniform the larvae were segregated according to their stage of development as determined by head capsule size. The number of larvae per collection ranged from 21 to 390, depending upon their abundance.

In addition to the representative larval collections, larvae on which dipterous parasites had deposited eggs externally were collected and reared individually in 90-by-20-mm. vials to provide information on their life-histories and habits.

Larval collections were placed in rearing cages in an unheated insectary. Each cage was 12 by 12 by 18 inches and was covered on the top and three sides with No. 80 cheesecloth. A sliding front of plastic one-sixteenth of an inch thick provided easy access. Alder foliage was supplied as required for food.

Each cage was examined daily and dead host larvae and parasite larvae were removed. All parasites obtained as larvae or pupae were placed in cotton-stoppered 90-by-20-mm. glass vials until the parasite adults emerged. Dead host larvae that did not contain parasites were shipped to the Entomology Laboratory, Kingston, Ontario, for pathogenic examination.

Pupae were collected from the infested area at frequent intervals from the time pupation started until moth emergence was complete, to obtain information concerning parasitism in all stages of pupal development. The number of pupae per collection ranged from 4 to 186. Pupae were reared in two types of containers. Some were reared individually in 90-by-20-mm. glass vials to obtain information on parasite relationships and the numbers of each parasite species that emerge from a single host. The remainder were reared in wooden cages, 11 by 14 by 3 inches, with a sliding glass top for easy access and cotton-covered perforations in the ends for ventilation. The bottoms were covered with white blotting paper, which was moistened if required to prevent desiccation of the pupae. After its publication, dipterous puparia were determined to species by the key by Ross (1953).

Records of emergence of host adults and parasite larvae and adults were tabulated by species for each collection and the mortality/survival ratios calculated (Bess, 1945). Because the parasite species obtained from the various stages of the hosts overlapped, it was impossible to calculate the total reductive effect of the parasites on the host populations. The relative importance of each parasite species was determined by dividing the mortality/survival ratio by the mortality/survival ratio plus one, and multiplying the quotient by 100 which is designated by Bess (*loc. cit.*) as "relative percentage equivalent."

RESULTS AND DISCUSSION

During the period of the investigation disease was not an important control factor. Both virus and bacterial disease organisms were present in the *Malacosoma* spp. populations and, although there was high mortality among the confined larvae in some of the caged collections, there was no evidence of any unusual larval mortality in the infested areas.

The effect of vertebrate and invertebrate predators was not investigated, but field observation showed that more pupae were destroyed by predators in 1953 than in 1950, 1951, or 1952. Tothill (1918) stated: ". . . most of the larvae [*Malacosoma* spp.] from twenty-four egg masses that I had under observation there were eaten by spiders."

The numbers of eggs, larvae, and pupae of *Malacosoma* spp. and the numbers and percentages of parasites that were reared from them during 1950 to 1953 are shown in Table I. The period was one of rapidly increasing host populations. If the parasites had increased at the same rate as the host insects, the percentage parasitism would have remained the same each year. There was, however, no evident increase in total parasitism from 1950 to 1953.

TABLE I

PARASITISM OF VARIOUS STAGES OF *Malacosoma disstria* HBN. AND *M. pluviale* (DYAR) IN THE LOWER FRASER VALLEY B. C., 1950 TO 1953.

STAGE	YEAR	NUMBER OF HOSTS	NUMBER OF PARASITES	PER CENT PARASITISM[1]
Egg	1951	48,000	1,252	2.5
	1952	56,300	1,623	2.8
	1953	78,400	4,100	5.3
Larva	1950	990	237	19.3
	1951	585	352	37.6
	1952	1,700	458	21.2
	1953	3,064	414	15.6
Pupa	1950	50	116	69.9
	1951	142	262	64.9
	1952	398	139	25.9
	1953	997	232	23.3

[1] Based on the total number of parasites and surviving hosts.

Table II shows that from 1951 to 1953 there was an important increase in the number of hymenopterous parasites in relation to that of dipterous parasites. The populations of some hymenopterous species

TABLE II

NUMBERS OF *Malacosoma* SPP. PARASITIZED BY DIPTEROUS AND HYMENOPTEROUS PARASITES FROM 1951 TO 1953.

YEAR	DIPTERA	HYMENOPTERA[1]	TOTAL	PER CENT HYMENOPTERA
1951	556	57	613	9.3
1952	490	84	574	14.6
1953	375	236	611	38.6

[1] Not including egg parasites.

increased faster than others, and some dipterous species decreased but others increased. Hence the species of parasites obtained in 1952 and 1953 were grouped according to their life-histories (some of the species obtained in 1951 were not identified and the data for that year could not be used). The dipterous species that have only one generation per year and do not require a host other than *Malacosoma* spp. were placed in Group 1; those that have two or more generations per year and require a host other than *Malacosoma* spp. to complete their seasonal history were placed in Group 2. The hymenopterous species were grouped according to the stage of the host that they parasitize. Those that parasitize third-, fourth-, and early-fifth-instar larvae were placed in Group 3, and those that parasitize late-fifth-instar, prepupal, and pupal stages were placed in Group 4. The species in each group were:

Group 1
Carcelia malacosomae Sell.
Rileymyia triseta Brks.
Sarcophaga aldrichi Park.
Sarcophaga houghi Ald.
Tachinomyia similis (Will.)

Group 2
Achaetoneura frenchii (Will.)
Compsilura concinnata (Mg.)
Euexorista futilis (O. S.)

Group 3
Hyposoter fugitivus pacificus Cush.
Phobocampe sp.
Rogas sp.

Group 4
Bracon xanthonotus Ashm.
Itoplectis viduata (Grav.)
Labrorychus analis (Say)
Pimpla pedalis Cress.
Pimpla sanguinipes Cress.
Theronia atalantae Poda

The numbers and percentages of individuals in each group were:

	Group 1	*Group 2*	*Group 3*	*Group 4*
1952	163, 33.3	49, 13.1	22, 26.2	62, 73.8
1953	326, 86.9	327, 66.7	100, 42.4	136, 57.6

The increase in the proportion of single-generation Diptera illustrates the effect of density-dependent factors on parasite populations. The dipterous species that have only one generation per year had abundant hosts (*Malacosoma* spp.), whereas those that have two or more generations per year were dependent upon hosts that were less abundant than *Malacosoma* spp.

There was an increase in the percentage of early-larval parasites and a decrease in the hymenopterous late-larval and pupal parasites, probably because of competition. The hymenopterous early-larval parasites emerged from the hosts before parasitism by *Sarcophaga* spp. occurred, but many of the late-larval and pupal parasites were killed by *S. houghi* and *S. aldrichi*.

The primary parasites that were reared from *M. disstria* and *M. pluviale* and their relative percentage equivalents are given in Figure 1.

Notes on Life-histories and Habits

Notes on the life-histories and habits of each of the primary and secondary parasite species that were reared from *M. disstria* and/or *M. pluviale* follow.

HYMENOPTERA

Braconidae

Bracon xanthonotus Ashm.—The life-history of this species as a parasite of the omnivorous looper, *Sabulodes caberata* Gn., was described by McKenzie (1935). In the lower Fraser Valley, *B. xanthonotus* attacked only fifth-instar larvae of *Malacosoma* spp. If the parasites paralyze this host before ovipositing, the paralysis is temporary (*contra* McKenzie, *loc. cit.*). The larvae of *Malacosoma* spp. complete their development and spin their cocoons before they are killed by the parasite. The parasite cocoons are formed inside the host cocoon. Some of those reared from *Malacosoma* spp. remained in the pupal stage as long as 25 days. The maximum number of *B. xanthonotus* adults that were obtained from a *Malacosoma* sp. larva was 50 and the average was 35, as compared with an average of 18 to 22 from *S. caberata*.

Other hosts of *B. xanthonotus*, listed by Muesebeck and Walkley (1951), are: a tussock moth, *Hemerocampa oslari* Barnes; the western tussock moth, *H. vetusta* (Bdvl.); the blue-sided tent caterpillar, *Malacosoma constrictum* (Stretch); the great basin tent caterpillar, *M. fragile* (Stretch); and *Sabulodes* sp.

Rogas sp.—This species is primarily a parasite of fourth-instar larvae of *Malacosoma* spp. Larvae of *Malacosoma* spp. do not develop beyond the instar in which they are parasitized by this species. The larva of *Rogas* sp. pupates within the host larva after attaching its interior ventral surface to the substratum. The adult emerges in two to three weeks from a small circular hole cut in the posterior dorsal surface of the host.

Ichneumonidae

Atractodes sp.—This species is a secondary parasite that was obtained from *Sarcophaga aldrichi* Park. and *Sarcophaga houghi* Ald., primary parasites of *Malacosoma* spp. *Atractodes* sp. parasitizes the *Sarcophaga* spp. larvae and the adult emerges in mid-August through a large irregular hole cut in the anterior dorsal surface of the host puparium.

Hyposoter fugitivus pacificus Cush.—This species is an internal parasite that parasitizes fourth-instar larvae of *Malacosoma* spp. The host does not develop beyond the instar in which it is parasitized by this species. By the time that *H. fugitivus pacificus* completes its larval development, the unparasitized host larvae are in the fifth-instar. The pupa is enclosed in a silken cocoon within the host integument, which is split along the ventral surface. The parasite cocoon protrudes through the slit and is attached to the substratum. About 10 days after pupation, the parasite emerges through a hole cut in either the anterior or the posterior surface of the host.

In the lower Fraser Valley, *H. fugitivus pacificus* has been reared by the authors also from the rusty tussock moth, *Notolophus antiquus* (L.). Parasite adults emerge from *N. antiquus* during late August, approximately two months later than they emerge from *Malacosoma* spp., and it is presumed that *N. antiquus* is host to a second generation of the parasite. Other hosts have been reported by Townes and Townes (1951). Essig (1926) reports *H. fugitivus pacificus* to be the western form of *Hyposoter fugitivus fugitivus* (Say).

Itoplectus viduata (Grav.).—This species is a relatively unimportant pupal parasite of *Malacosoma* spp. Only three specimens were obtained during this investigation.

Labrorychus analis (Say).—This species is an internal parasite reared from fifth-instar larvae and pupae of *Malacosoma* spp. *L. analis* adults emerge within a short time after host pupation and it is presumed that only larvae were parasitized. The larva, when mature, forms a thin membranous cocoon, which is surrounded by and attached to the host pupal case by coarse but sparse webbing. The parasite pupa is enclosed in a thin gelatinous membrane, which is probably the pre-pupal cuticle (Wigglesworth, 1950). This membrane protects the parasite during metamorphosis from the liquid excrement that surrounds the pupa. Adults emerge from the host pupae from mid-July to mid-August. Only one generation of *L. analis* adults was reared from *M. disstria* and *M.*

pluviale, but Schaffner and Griswold (1934) report that it has two generations and several other hosts, including: a species of tiger moth. *Cycnia tenera* Hbn.; the poplar tent maker, *Melalopha inclusa* Hbn. (*Ichthyura inclusa* Hbn.); the white-marked tussock moth, *Hemerocampa leucostigma* (A. & S.); and the eastern tent caterpillar, *Malacosoma americanum* (F.).

Phobocampe sp.—This species is primarily a parasite of fourth-instar larvae of *Malacosoma* spp., although a few specimens emerged from fifth-instar larvae. The larva of *Phobocampe* sp. emerges from the larva of *Malacosoma* spp. during the latter part of June and immediately spins a small oval cocoon. The parasite remains as an active larva within the cocoon for two to three days but pupates and emerges by mid-July.

Schaffner and Griswold (1934) state that *P. clisiocampae* (Weed) has two generations per year and overwinters in its cocoon. These workers obtained *P. clisiocampae* from the prominents *Datana perspicua* G. & R. and *Schizura concinna* A. & S.; *H. leucostigma; M. americanum*; *M. disstria*; and the fall cankerworm, *Alsophila pometaria* (Harr.).

Pimpla pedalis Cress. and *P. sanguinipes* Cress.—These species are primarily pupal parasites of *Malacosoma* spp. Examination of one *Malacosoma* sp. pupa from which *P. pedalis* had emerged revealed that the entire contents of the host pupa had been consumed and the pupal shell lined sparsely with coarse webbing. The adults of *Pimpla* spp. emerge from the *Malacosoma* spp. pupae from early to mid-August.

Schaffner and Griswold (1934) state that *P. pedalis* has two or more generations per year and overwinters in the host pupa. They list the following hosts: larvae of a species of tiger moth, *Halisidota* sp.; a prominent, *Heterocampa guttivitta* (Wlk.); *H. leucostigma;* and *M. americanum.* Essig (1926) lists several species on which *P. pedalis* is parasitic, including *M. disstria. P. pedalis* has also been obtained by the authors from the oak looper, *Lambdina somniaria* (Hulst), on Vancouver Island.

Theronia atalantae (Poda).—This species is primarily a pupal parasite of *Malacosoma* spp. Before pupating in late July, the *T. atalantae* larva consumes the entire contents of the host pupa and spins a coarse but open cocoon on the interior surface of the host pupal case. It emerges as an adult from early to mid-August and is the last primary hymenopterous parasite to emerge from *Malacosoma* spp. in the Fraser Valley.

Essig (1926) states that *T. atalantae* is probably a secondary parasite, through *Iseropus coelebs* (Walsh), *Itoplectis conquisitor* (Say), or *P.*

pedalis, on various species of tussock moths, *Hemerocampa* spp.; tent caterpillar species, *Malacosoma* spp.; the spruce budworm, *Choristoneura fumiferana* (Clem.), and other Lepidoptera. However, in the Fraser Valley *T. atalantae* is primary in all *Malacosoma* spp. pupae that have been examined. In 1953 three specimens of external secondary hymenopterous larvae were observed feeding on *T. atalantae*. The identity of these secondary parasites is not known.

Chalcidoidae and *Proctotrupoidea*

Ooencyrtus clisiocampae (Ashm.), *Telenomus clisiocampae* Ril., *Tetrastichus malacosomae* Gir., and *Tetrastichus silvaticus* Gahan were reared from egg masses of both *M. disstria* and *M. pluviale*. These species deposit their eggs in those of *Malacosoma* spp. shortly after moth oviposition in late July and early August. The parasites complete their larval development and remain in the eggs in the mature larval stage over winter. Adults emerge during June and July.

Tritneptis sp.—This species was reared from pupae of *Malacosoma* sp. and the parasite adults emerged from mid-August to early September. Remains of dipterous parasite larvae were found in some of the pupal shells of *Malacosoma* sp., indicating that *Tritneptis* sp. was a secondary parasite. In other pupal cases from which this species emerged there was no evidence of parasitism by other species.

The numbers of *Tritneptis* sp. that were obtained from single pupae of *Malacosoma* sp. ranged from 6 to 102.

DIPTERA

Tachinidae

Species of the Family Tachinidae were the most important parasites of *M. disstria* and *M. pluviale* larvae. Though some of the species are single-brooded and others multiple-brooded, they all have similar life-cycles when parasitic on *Malacosoma* spp. larvae.

Achaetoneura frenchii (Will.).—This species parasitizes fifth-instar larvae of *Malacosoma* spp. The parasite larvae emerge from the host during the latter part of June or early July and form puparia within 24 hours. The adults emerge from the puparia approximately three weeks later. Schaffner and Griswold (1934) report that this species parasitizes 29 identified and two unidentified species of lepidopterous larvae; that it has two or more generations per year; and that as many as 27 individuals have been obtained per host. In these studies only one individual per host larva was obtained.

Carcelia malacosomae Sell.—This species deposits small, white, elongate, pedicellate eggs on exposed surfaces of *Malacosoma* spp. larvae.

The female usually oviposits on fourth-instar larvae and many eggs are destroyed through the moulting of the host larvae. From a collection of 19 larvae of *M. disstria* on which *C. malacosomae* eggs had been deposited, three of the larvae moulted before the eggs had hatched. Of the remaining 16 larvae, five were unparasitized. Although as many as three eggs have been observed on one host larva, only one parasite develops per host.

C. malacosomae larvae emerge from *Malacosoma* spp. during the first part of July. They overwinter as pupae.

Compsilura concinnata (Mg.).—This species was introduced into British Columbia for the control of the satin moth, *Stilpnotia salicis* (L.); a total of 2,236 adults were released in the Fraser Valley between 1929 and 1934 (McLeod, 1951). In addition to its original host, *S. salicis,* it has been reared from the tent caterpillars *M. disstria* and *M. pluviale*; the rusty tussock moth, *Notolophus antiquus* (L.); and the fall webworm, *Hyphantria cunea* (Drury). *C. concinnata* has an extremely wide host range, having been recorded from 194 hosts by Thompson (1951, pp. 53–57). It is probably parasitic on many other species of Lepidoptera in the lower Fraser Valley in addition to those recorded in these studies.

C. concinnata has three generations per year in the lower Fraser Valley. The first generation develops in the larvae of *M. disstria, M. pluviale,* and *S. salicis.* Adults emerge during July and parasitize the larvae of *N. antiquus.* The second-generation adults parasitize the larvae of *H. cunea during* September. When the *C. concinnata* larvae are fully developed they form their puparia and pass the winter in the pupal stage.

The effectiveness of *C. concinnata* as a control agent for *Malacosoma* spp. is probably determined by the abundance of third-generation hosts and the availability and abundance of first generation alternate hosts.

Euexorista futilis (O. S.).—This species was obtained from fifth-instar larvae and pupae of *Malacosoma* spp. The mature larvae emerge from *Malacosoma* spp. during July and pupate at once. The adults emerge approximately three weeks later. Laboratory-reared second-generation adults were observed mating during late August and dissection of a fertilized female revealed numerous fully developed small, oval, white eggs. It is presumed, therefore, that this species has at least two generations per year and that hosts other than *Malacosoma* spp. are essential.

Patelloa sp.—Specimens of this species were obtained from one collection of *M. pluviale* in 1952 only. The mature larvae emerged from the host about mid-July and pupated immediately. The date of adult emergence is not known because the pupae died in the puparia during winter storage.

Rileymyia triseta Brks.—This species was described as new in 1946 by Brooks (1946). The holotype and allotype specimens in the Canadian National Collection, Ottawa, were collected in 1916 at Victoria by R. C. Treherne. At that time the species was known as *Blepharipeza* sp. and it was one of the most important parasites of *Malacosoma* spp. in British Columbia. The population of *R. triseta* increased more rapidly than that of any other parasite species from 1950 to 1953.

R. triseta has been obtained from both *M. disstria* and *M. pluviale* but only from collections of fifth-instar larvae and pupae. It emerges as a larva from the host pupa from late June to mid-July and overwinters as a puparium. Adults emerged in the laboratory during April.

Tachinomyia similis (Will.).—This species deposits relatively large white eggs on or near the head of *Malacosoma* spp. larvae. The ventral surface of the egg is flattened and is attached firmly to the host. The parasite usually oviposits on fifth-instar larvae and eggs are not destroyed through the moulting of the host larvae. However, from a collection of 42 larvae of *M. pluviale* on which eggs had been deposited, only 32 adults of *T. assimilis* emerged, indicating that some of the parasites fail to become established in the host. As many as four eggs were observed on one host larva but no record of more than one adult emerging from a larva was obtained.

T. assimilis larvae emerge from *Malacosoma* spp. from late June to mid-July, and after forming their puparia pass the winter in the pupal stage.

Sarcophagidae

Sarcophaga aldrichi Park.—Hodson (1939) states that *S. aldrichi* deposits larvae on the cocoons of *M. disstria*. The larvae enter the cocoons and attack the host pupae, destroying them and also any hymenopterous or other dipterous parasites that are present. If the weather is favourable, *S. aldrichi* completes larval development in 8 to 12 days. The puparia are formed in the soil and the pupae remain in diapause throughout the winter.

In 1951 *S. aldrichi* larvae were obtained from host pupae containing the remains of hymenopterous parasites, and in 1953 *S. aldrichi* larvae emerged from two puparia of *Carcelia malacosomae* Sell. The puparia of the latter were malformed, suggesting that the presence of *S. aldrichi* had interfered with their normal formation. The extent of secondary parasitism or predation by *S. aldrichi* is not known, but this species may be an important agent in limiting increases in the populations of the other pupal parasites of *Malacosoma* spp.

Laboratory rearing also revealed considerable variation in the time that *S. aldrichi* larvae form their puparia. Some larvae formed their puparia within a few hours after leaving the host but most of them did not form their puparia for several weeks.

Sarcophaga houghi Ald.—This species is also a pupal parasite of *M. disstria* and *M. pluviale* and, as with *S. aldrichi,* there was considerable variation in the rate of development. Some larvae pupated shortly after leaving the host, whereas others remained in the larval stage and did not form their puparia for several weeks. Unlike *S. aldrichi,* some of the *S. houghi* larvae that pupated a short time after leaving the host continued to develop and adults emerged in August, about three weeks after pupation.

SUMMARY

From 1950 to 1953 there was a rapid increase in the populations of the tent caterpillars *Malacosoma disstria* Hbn. and *Malacosoma pluviale* (Dyar) in the lower Fraser Valley of British Columbia. From representative collections of eggs, larvae, and pupae obtained during the three years, 23 species of primary and secondary parasites were reared; and of these, 14 species were Hymenoptera and 9 were Diptera. In 1950 the dipterous parasites were much more numerous than the hymenopterous parasites. By 1953 the hymenopterous parasites had increased but were still fewer than the dipterous parasites. The hymenopterous species that increased most rapidly were those that completed their development and emerged from the host larvae or pupae before they could be destroyed by sarcophagid larvae. The species of dipterous parasites that became abundant as the tent caterpillar infestation intensified were those that have a single generation per year. The populations of the species that require alternate hosts to complete their life-cycles were apparently restricted by the scarcity of alternate hosts.

ACKNOWLEDGMENTS

Dipterous puparia were identified by D. A. Ross, Forest Biology Laboratory, Vernon, B. C. Adult parasites and hosts were determined by officers of the Systematic Entomology Unit, Entomology Division, Ottawa, as follows: Diptera, G. E. Shewell; Hymenoptera, O. Peck, G. S. Walley, and W. R. M. Mason; and Lepidoptera, T. N. Freeman. Diseases of the host larvae were identified by G. E. Bucher, Officer-in-Charge, Entomology Laboratory, c/o Queen's University, Kingston, Ontario. The assistance of these officers of Science Service is gratefully acknowledged.

References

Baird, A. B. (1917): An Historical Account of the Forest Tent Caterpillar and the Fall Webworm in North America. *47th Ann. Rept. Ent. Soc. Ontario*, 1916, pp. 73-84.

Bess, H. A. (1945): A Measure of the Influence of Natural Mortality Factors on Insect Survival. *Ann. Ent. Soc. Am.*, 38, 472-481.

Brooks, A. R. (1946): A Revision of the North American Species of *Leschenaultia sens. lat.* (Diptera, Larvaevoridae). *Canadian Ent.*, 78, 169-182.

Essig, E. O. (1926): Insects of Western North America. New York, Macmillan.

Glendenning, R. (1923): Insects of Economic Importance in the Fraser Valley in 1921. *Proc. Ent. Soc. British Columbia*, Econ. Ser. 17 and 19, 167-172.

Hodson, A. C. (1939): *Sarcophaga aldrichi* Parker as a Parasite of *Malacosoma disstria* Hbn. *J. Econ. Ent.*, 32, 396-401.

McKenzie, H. L. (1935): Biology and Control of Avocado Insects and Mites. *Univ. California Agr. Expt. Sta. Bull.* 592, 20-21.

McLeod, J. H. (1951): Biological Control Investigations in British Columbia. *Proc. Ent. Soc. British Columbia*, 47, 27-36.

Muesebeck, C. F. W. and Luella M. Walkley (1951): Family Braconidae. *In* Hymenoptera of America North of Mexico. Synoptic Catalog, by C. F. W. Muesebeck, K. V. Krombein, H. K. Townes, and others. *U.S. Dept. Agr., Agr. Monogr.* 2, 90-184.

Ross, D. A. (1953): Key to Puparia of the Dipterous Parasites of *Malacosoma* spp. in British Columbia. *Proc. Ent. Soc. British Columbia*, 49, 19-23.

Schaffner, J. V. and C. L. Griswold (1934): Macrolepidoptera and Their Parasites Reared from Field Collections in the Northeastern Part of the United States. *U.S. Dept. Agr. Misc. Pub.* 188, 150.

Thompson, W. R. (1951): A Catalog of the Parasites and Predators of Insect Pests. Section 2, Host Parasite Catalogue. Part 1, Hosts of the Coleoptera and Diptera.

Tothill, J. D. (1918): Natural Control Investigations in British Columbia. *Proc. Ent. Soc. British Columbia*, Systematic Ser. 12, 37-39.

Townes, H. and Marjorie Townes (1951): Family Ichneumonidae. *In* Hymenoptera of America North of Mexico. Synoptic Catalog, by C. F. W. Muesebeck, K. V. Krombein, H. K. Townes, and others. *U.S. Dept. Agr., Agr. Monogr.* 2, 184-409.

Twinn, C. R. (1938): A Summary of the Insect Pest Situation in Canada in 1937. *68th Ann. Rept. Ent. Soc. Ontario*, 1937, pp. 72-86.

———. (1942): A Summary of the More Important Crop Pests in Canada in 1941. *72nd Ann. Rept. Ent. Soc. Ontario*, 1941, pp. 47-56.

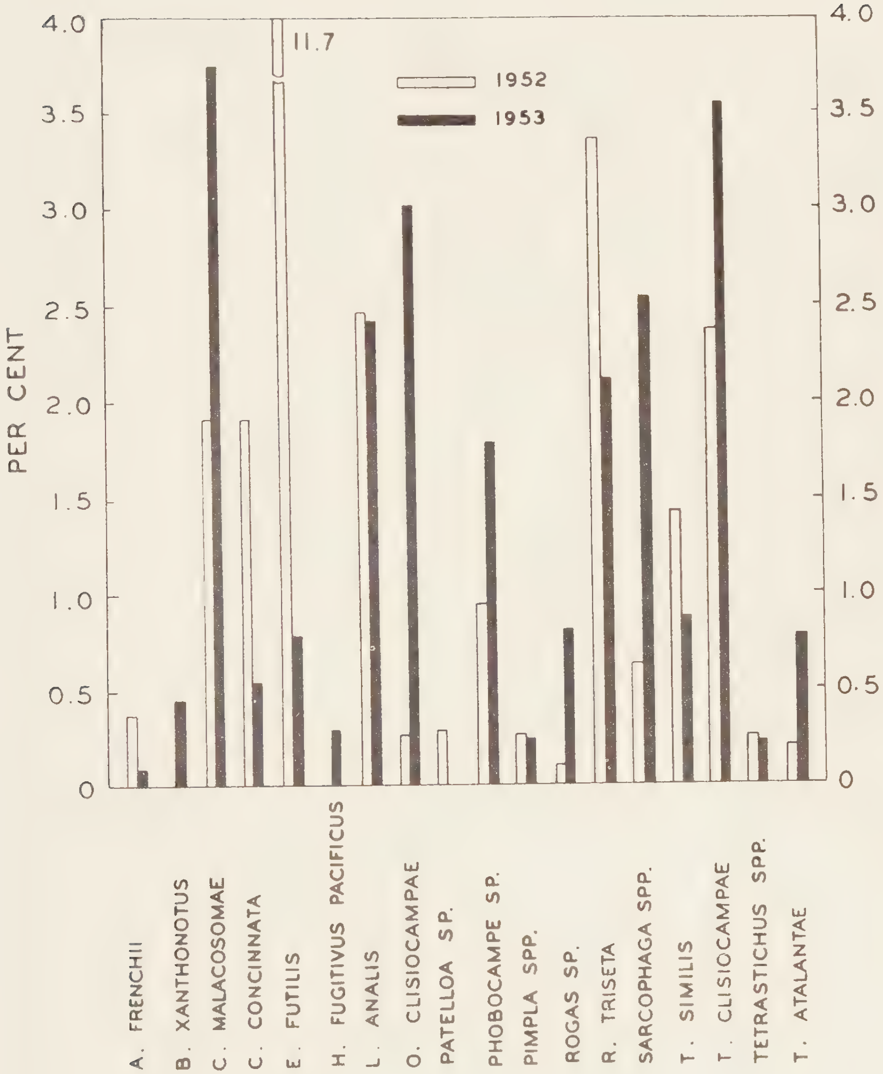


FIGURE 1.—Relative percentage equivalents of parasites attacking *Malacosoma* spp. in the Fraser Valley in 1952 and 1953 ("relative percentage equivalents" of Bess, 1945).

EUROPEAN AGRIOTES WIREWORMS (ELATERIDAE) FOUND ESTABLISHED IN COASTAL BRITISH COLUMBIA, CANADA

By K. M. King and A. T. S. Wilkinson
Entomology Division, Science Service
Department of Agriculture
Victoria, B. C. Canada

Abstract

The destructive European wireworms *Agriotes obscurus* L. and *A. lineatus* L., have long been known to occur in the eastern Maritime Provinces of Canada, but their presence in the Pacific Northwest was not discovered until 1949. In that year an intensive but localized infestation, chiefly *A. lineatus,* was found in an isolated valley on southern Vancouver Island, British Columbia. In 1952, severe damage to corn, following pasture, led to the discovery of an important infestation of *A. obscurus* on several farms near Agassiz, on the lower mainland of this Province. There are strong indications that both infestations have been present for several decades, though hitherto unrecognized. Fortunately, the hazard of distant spread from the presently known infestation seems small—if even modest precautions are taken—when consideration is given to the agricultural isolation of both localities in relation to the known habits of these species. Survey is being extended to other parts of the region, and experiments on chemical control are in progress.

THREE FRUIT FLIES (TEPHRITIDAE) OF ECONOMIC IMPORTANCE IN HAWAII[1]

By Henry A. Bess and Toshiyuki Nishida
Agricultural Experiment Station
College of Agriculture, University of Hawaii
Honolulu, Hawaii

Fruit flies (the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), the melon fly, *Dacus cucurbitae* Coquillett, and the oriental fruit fly, *Dacus dorsalis* (Hendel) are the worst pests of certain fruits and vegetables grown in Hawaii. Furthermore, since these flies do not occur on the mainland United States their presence has made it necessary to ban these fresh fruits and vegetables from shipment to mainland markets. Therefore, the losses from these flies to Hawaii cannot be readily estimated, but the flies have a tremendous effect on the economy of the islands.

Of the three species involved, two are pests of fruits such as guavas, and the other of tomatoes and cucurbits. From the standpoint of local production of agricultural crops, the melon fly which attacks tomatoes and cucurbits causes greater damage than the combined damage caused by the Mediterranean and oriental fruit flies.

The purpose of this paper is to give an account of the economic importance and status of these flies in Hawaii and the basic information now available on their biology and control.

The Mediterranean Fruit Fly, Ceratitis Capitata (Wiedemann)

The Mediterranean fruit fly is a common pest in the countries bordering the Mediterranean and occurs elsewhere in various parts of Africa, Australia and Hawaii, but apparently does not occur in other countries in the central and north Pacific. It became established in Hawaii in 1910 and immediately became a serious pest of fruits throughout the islands. Several parasites were introduced to combat the fly but for the next 35 years it continued to be a formidable pest of fruits in the more tropical lowland areas as well as in the deciduous fruit areas at higher elevations on Maui and Hawaii. Following the establishment and build up of the oriental fruit fly, *Dacus dorsalis*

---

[1] Published with the approval of the Director of the Hawaii Agricultural Experiment Station as Misc. Paper No. 55.

Hendel, *C. capitata* ceased to be a problem in the lowlands but has continued to cause damage to certain fruits in the more temperate areas at higher elevations.

Economic Importance

The principal damage caused by *C. capitata* in recent years has been limited primarily to stone fruits, loquats, and persimmons grown in the more temperate climatic zones on Maui and Hawaii. Unless effective sprays are applied, practically all persimmons, loquats, apricots, peaches, and certain varieties of plumps grown in these areas become infested and worthless. However, the fly is no longer a problem in the production of bananas, papayas, mangoes, guavas, and avocadoes grown at low elevations.

Since *C. capitata* does not occur on the mainland of the United States and might cause tremendous damage should it become established there, the occurrence of this fly in Hawaii creates a trade barrier from the standpoint of the shipment of fresh fruits to the mainland. Therefore, this fly is a great deterrent to the development of a market for Hawaiian fruits and the expansion of the fruit industry in Hawaii.

Habits and Seasonal Abundance

Adults of *C. capitata* are rather secretive and inconscpicuous in orchards. They tend to remain inactive on the underside of leaves most of the time except when ovipositing. Consequently, considerable damage may occur even when very few flies are seen in the orchards.

Females tend to oviposit in the softer blossom end of peaches as they ripen. Gelatinous sap usually exudes from the oviposition punctures in stone fruits and there is often a reduction in the growth of the fruit around the puncture resulting in deformity. The females oviposit in immature persimmons which turn dark around the punctures, but the larvae are unable to develop. Ripe fruits, if left on the trees, are more attractive than green fruits for oviposition. However, relatively few larvae complete their development in fruits picked at the stage of ripeness desired for market.

Flies apparently remain in orchards and nearby vegetation for weeks after emergence, even though there is no fruit around. Furthermore, it appears that the flies that attack persimmons in the fall are those that bred earlier in the season in loquats or peaches.

Data are available which show that *C. capitata* is more abundant above 1,500 to 2,000 feet elevation than below 500 feet elevation (Bess, 1953). Some of these data also indicated that this fly was more abundant in the spring and early summer at elevations between 500 and 2,500 feet than at other seasons.

Control

Biological control

Since *C. capitata* became scarce or absent in lowland areas within a year or so after *D. dorsalis* became established in Hawaii, it appears that the latter species of fruit fly was responsible in some way for the reduction of the former one. We are not sure as to whether or not there was a decline in the abundance of *C. capitata* at higher elevations during the same period. However, following the establishment of *Opius oophilus* Fullaway, a braconid parasite of *D. dorsalis*, there has been a decline in the abundance of *C. capitata* in these upland areas. Parasitization commonly exceeds 50 percent.

Chemical control

Experimental spray tests, as well as regular orchard spraying done by orchardists, have shown that this fly can be effectively controlled on persimmons by spraying with DDT. The sprays were applied with a power sprayer at a concentration of 2 pounds of 50 percent wettable DDT per 100 gallons of water. However, it was necessary to spray all trees that may harbor flies in the orchard and vicinity, even though they may be free of fruits. All trees should be sprayed thoroughly immediately before the fruits become attractive to the flies for oviposition. The necessity for subsequent spraying will depend upon the immigration of flies into the orchards.

THE MELON FLY, DACUS CUCURBITAE COQUILLETT

In many countries in the Pacific area the melon fly is well known. This insect, first officially reported in the Hawaiian Islands in 1898 (Clark, 1898), was described in 1899 by Coquillett from specimens reared from cucumbers in Honolulu. Since then it has been reported from tropical to subtropical areas of the Pacific, among which are northern China, Formosa, India, Malaya, the Philippines, northern Australia, Mauritius, Kenya, and the Hawaiian Islands.

Economic Importance

The melon fly is a pest of various crops, principally melons, cantaloupes, squashes, cucumbers, and tomatoes. The eggs are deposited in fruits and soft tissues of vegetative parts of certain plants, particularly those in the family Cucurbitaceae. After hatching, the larvae burrow into the plant tissue. As the result of the larval feeding and also decomposition caused by secondary microorganisms the tissues attacked are quickly destroyed. Occasionally, the larvae fail to develop and decomposition may cease; however, the fruits involved are much reduced in market value because of the deformity. Larvae fail to develop in young tomatoes but the fruits are often destroyed by rot organisms.

The extent of damage caused by the melon fly is well documented ever since it was first discovered in the Hawaiian Islands. Two years after its discovery 75 percent of the melons, cantaloupes, and cucumbers were destroyed (Howard, 1900). In 1914 the estimated losses resulting from melon fly attack amounted to millions of dollars (Severin, *et al.,* 1914). During 1918 the crop loss was estimated to be in the neighborhood of 3/4 million dollars (Back and Pemberton, 1818).

Studies made during 1951 in commercial plantings showed that the infestation of young cucumbers and tomato fruits at Waimanalo ranged from 10 to 100 percent and 2 to 40 percent, respectively. At Waianae the infestation of cucumbers ranged from 5 to 60 percent and that of young tomatoes, 2 to 70 percent. Observations made at elevations above 2,500 feet showed that the general level of infestation was lower in these high elevations than in coastal areas.

That the melon fly is a serious pest which has defied control measures is evidenced by the type of control measures practiced to a certain extent even today in an era when highly toxic insecticides, heretofore unknown, are available. Melon growers frequently cover each fruit, before it is stung, with sheets of newspaper or burlap sacking to prevent damage. In addition to these time consuming practices growers often spray their crops as frequently as twice a day. With such practices it is indeed not surprising that the price of melons reaches as high as 30 to 40 cents per pound in Honolulu markets.

The economic importance of the melon fly lies not only in its direct promulgated by state and federal governments in the United States and effects, but also in its indirect effects. Quarantine laws have been also by governments of other countries to prevent the introduction and establishment of the melon fly into new areas. Although data on the amount spent on quarantine control are not available, it is evident that the melon fly has played an important role in the economy of the countries involved. To such countries, as for example the United States where attempts are made to prevent its introduction, it means a considerable expenditure of funds to maintain an efficient quarantine system. To other areas, as for example the Hawaiian Islands, it means a trade barrier which reduces the number of products to be exported. To some extent this trade barrier has been broken in recent years through commodity treatments, but these treatments often adversely affect quality and increase the cost of the product. The loss of quality and increased cost would place the products in question in an unfavorable competitive position in relation to similar products from other areas (Bird, 1952).

Biology and Ecology

There is considerable information on the biology and ecology of the melon fly, but no attempt is made to present an exhaustive treatment of these subjects. Only those aspects dealing with generalized life history and those dealing with ecology which are of importance from the standpoint of the control of the insect are presented.

The following account represents a generalized life history observed under conditions prevailing in the coastal areas of the Hawaiian Islands. The female fly punctures the host tissue by means of her ovipositor and makes a cavity into which eggs are deposited. The larvae, which hatch from these eggs in about 1 to 2 days, feed and burrow deeper and deeper into the host tissue. Prior to pupation the full grown larvae enter the soil where they pupate at depths of 2 to 3 inches. Within about 10 days the adults emerge from the puparia and force their way to the surface of the soil. Upon reaching the surface they remain motionless in sheltered spots, such as under rocks and débris, until their bodies harden; then they move on to various plants where they spend the greater part of their adult life.

The adults are closely associated with certain plants. In localities where the insect occurs there are many kinds of plants; however, the flies are found among relatively few of the plants. Weed species attractive to the flies include castor bean (*Ricinus communis* L.), cocklebur (*Xanthium saccharatum* Wall.), spring amaranth (*Amaranthus spinosus* L.), Jimson weed (*Datura stramonium* L.), pigeon pea [*Cajanus cajan* (L.) Millsp.], and popolo (*Solanum nodiflorum* Jacq.). In addition, melon fly adults are closely associated with certain cultivated plants such as corn, beans, eggplants, and bell peppers.

Studies of the sex and age of the flies found on the host crop and other vegetation gave a good deal of information about the behavior or movement of the adults. In fields devoid of weeds the large part of the adult population was found among favorable plants which were often present along the edges of the field. Comparatively few flies were present within the field among crop host plants even though there were adults emerging from puparia in the soil beneath them. The number of adults within the crop area was generally small; but nearly all of them were gravid. Many more adults of both sexes and various ages were present among plants along the edges of the field. This difference in the composition of the population between the field and outside of the field was assumed to be due to the differential movement of adults of various ages. Newly emerged adults did not remain within the field among crop host plants where they emerged if the field was devoid of weeds attractive to them. As soon as they were able to fly, newly emerged adults moved out of the field in a series of short flights. Gravid females, on the other hand, moved into the field from the bordering vegetation. However, they did not remain in the field for long periods. All of the gravid females moved out of the field in the evening. Consequently, during the early morning hours and late in the evening hardly any adults were present among crop plants.

Seasonal trends in population of adults studied throughout the year 1951 showed a marked seasonal fluctuation even though the climate in the Hawaiian Islands is oceanic and displays relatively little seasonal variation. Melon fly abundance as measured by the extent of punctured tomato and cucumber fruits showed that the percentage of stung fruits was highest during the fall and winter months and lowest during the summer. The population measured by sweeping adults among favored plants showed almost identical seasonal trends.

Control

The control of the melon fly in the Hawaiian Islands has been undertaken by biological and chemical methods. Our present knowledge concerning these two methods of control are discussed in the following paragraphs.

Biological control

Parasites and predators have been introduced periodically into the Hawaiian Islands during the past fifty years. Among the many that were introduced, the most successful parasite that has become established is *Opius fletcheri,* which was introduced from India (Fullaway, 1919). Unfortunately, this species parasitizes melon fly larvae largely in the fruits of the wild *Momordica balsamina* Linn., but only to a very limited extent of the larvae in cultivated fruits in which large numbers of flies breed. Because of this failure, of *O. fletcheri* to destroy larvae in cultivated fruits, it cannot be relied upon to suppress the population to a point where no economic damage results.

Chemical control

Our present knowledge concerning the chemical control of the melon fly is the result of the diligent work of a number of investigators who have reported on various methods. The methods used by the earlier workers may be grouped as (1) use of mechanical protectants of fruits, as for example, sheets of burlap sacks, newspapers, or metal screens (Severin, *et al.*, 1914; Back and Pemberton, 1917), (2) use of poison baits to kill adults (Marsh, 1910; Severin, *et al.*, 1914; Back and Pemberton, 1917), (3) use of traps to capture and destroy adults (Severin, *et al.*, 1914; Back and Pemberton, 1917; McPhail, 1943), (4) use of residual sprays applied on crops and corn barriers (Holdaway, *et al.*, 1947).

The use of poison baits applied on crops and the use of traps failed to destroy enough of the adults to protect the crop concerned. The method of covering each fruit gives adequate fruit protection, but the procedure is laborious and costly. The use of residual sprays on crops and corn barriers has given adequate fruit protection in certain cases but not in others.

The more recent approach to the problem, which involves the utilization of information on fly behavior in the application of insecticides, has given promising results. The basis of insecticidal application lies in the behavior of the insect. As mentioned in the previous section, the population is higher outside of the field than within the field and gravid flies do not remain within the field for any extended period of time. Furthermore, field observations have shown that it was not always possible to control the melon fly by means of residual treatments made on the crops to be protected, a fact which was recently confirmed by Ebeling, *et al.*, (1953). In view of these considerations it appeared more logical to treat the surrounding vegetation rather than the crop. Spray experiments with DDT (Nishida and Bess, 1951) and parathion, DDT, and EPN (Ebeling, *et al.*, 1953) have shown that control can be obtained by treating the wild vegetation surrounding a field. For example, in a border treated tomato field the infestation was only 2 to 4 per cent, while in the nearby fields where crop treatments were made the infestation ranged between 63 and 68 per cent. An experiment carried out in a watermelon field showed that in the border treated field the infestation in the fruits less than 4 inches in diameter was 6.7 per cent, a figure which is exceedingly low when one considers the area in which the experiment was carried out. In the area concerned farmers were covering each fruit, otherwise, hardly any fruit escaped damage before they were 4 inches in diameter.

The present approach to the melon fly problem appears sound; it is not only effective, but it eliminates the problem of poisonous residues on the crop. This line of approach requires further investigation and studies are being made with the hope that eventually the melon fly will no longer be a major pest in the Hawaiian Islands.

The Oriental Fruit Fly, *Dacus dorsalis* Hendel

The oriental fruit fly occurs in India and in several countries in the Pacific, including Malaya, Java, the Philippines, Australia, and Hawaii. It was first discovered in Hawaii in the spring of 1947 and within a few months it was found on all of the islands and had become exceedingly abundant. Immediate steps were taken to find enemies of the fly and introduce them to combat the pest. In June of 1948, N. L. H. Krauss, entomologist with the Territorial Board of Agriculture and Forestry, began shipping fruit fly puparia containing parasites to Honolulu from Malaya and subsequently, seven agencies pooled their resources and participated in a world wide search for parasites and predators of fruit flies (Carter, 1950). Soon after liberation four of the Malayan species of braconid parasites became firmly established and three of them rapidly increased to tremendous numbers (Bess, van den Bosch and Haramoto, 1950; van den Bosch, Bess, and Haramoto, 1951). The peak in abundance of *D. dorsalis* was reached either in 1947 or in 1948, and within a year or so the fly became far less abundant than during the peak years. The fly is still a pest of certain fruits but a large percentage of fruits formerly damaged are free from attack without control measures applied.

Economic Importance

From 1947 to 1949 most of the edible fruits, such as mangoes, litchi, guavas, papayas, avocadoes, and bananas were usually so heavily infested that they were worthless. Even the thick skinned winter varieties of avocadoes, loquats, and persimmons grown between 3,000 and 5,000 feet were usually infested and unsalable. However, the situation improved rapidly after the parasites became established. During the past three seasons there has been very little damage to fruits above 3,000-foot elevation, but the fly is still a formidable pest of guavas, and in some instances of mangoes. Around 50 per cent of the guavas are commonly stung but possibly 90 per cent of the mangoes are free of attack. Papayas and bananas picked at the stage of ripeness demanded by the market are seldom infested.

From an economic standpoint, the loss of potential markets for Hawaiian fresh fruits due to the occurrence of *D. dorsalis* is of greater importance to Hawaii than the actual loss in fruit production due to the fly.

Habits and Seasonal Abundance

Adults of *D. dorsalis* are quite active and conspicuous in orchards. When abundant they commonly occur in dwellings and even downtown office buildings. They are also found in areas hundreds of yards from the nearest breeding sites and marked flies have been recovered several miles from the point of release (Carter, 1950). However, mass movements of flies have not been observed.

D. dorsalis breeds throughout the year in Hawaii, but there appears to be two fairly distinct peaks in abundance, a small one in the spring and a larger one in the fall. These peaks are associated with peaks in the abundance of guavas, the fruit which produces the larger part of the fly population in Hawaii.

Control

Biological control

The tremendous decrease in the abundance of *D. dorsalis* following the introduction and establishment of parasites has been phenomenal. Nevertheless, the fly still causes considerable damage to certain fruits in the lowlands.

There are three species of introduced parasites that have been important in the reduction or control of *D. dorsalis* in Hawaii. They are braconids, *Opius longicaudatus* (Ashmead), *O. vandenboschi* Fullaway, and *O. oophilus* Fullaway, which were introduced from Malaya during the summer of 1948. *O. longicaudatus* increased rapidly in the fall of 1948, became numerous within a few months, and parasitized around 25 to 35 per cent of the population. During the spring of 1949 *O. vandenboschi* also increased rapidly and by that fall was parasitizing far more maggots than *O. longicaudatus.* Parasitization by the two species together exceeded 80 per cent and hundreds of males were often seen in swarms (Bess, van den Bosch, and Haramoto, 1950). In December of 1949 *O. oophilus* was recovered for the first time from fruit collections made on Oahu. However, this species is very closely related to *O. vandenboschi* and it is possible that it was established before that time. Nevertheless, within a short time after its discovery in December, 1948, it rapidly gained supremacy over the two other species (van den Bosch, Bess, and Haramoto, 1951) and it has continued to be the dominant parasite for the past three years. Parasitization has usually exceeded 75 per cent and over 90 per cent of this has been caused by *O. oophilus.*

Parasites have been a major factor in the reduction of the population of *D. dorsalis* to a point where many kinds of fruits can be grown practically free from infestation. At the time of the parasite introductions the population of *D. dorsalis* was so high that practically no edible tree fruits could be utilized. Today *D. dorsalis* causes little to no damage to peaches, persimmons, and loquats or other fruits grown above 3,000 feet elevation. Furthermore, papayas, bananas, and avocadoes which are commonly picked for market when they are still firm, are seldom infested. Even mangoes picked when firm for market are seldom heavily infested; around 90 per cent or more of the fruits commonly escape attack. On the other hand, 50 per cent or more of the guavas, a fruit highly susceptible to *D. dorsalis,* are usually damaged by this fly. Therefore, biological control has been successful from the standpoint of fruits like papayas and bananas, but it has been inadequate on guavas.

Chemical control

Much experimentation has been carried out with chemicals for the control of *D. dorsalis* in guava woodlands and the results show promise of giving effective control (Steiner and Hinman, 1952). The infestation in mango, persimmon, loquat, and avocado orchards has not been sufficiently high in commercial orchards during the past three years to warrant systematic spraying or to give an opportunity to allow entomologists to run worthwhile spray tests in these orchards. However, the laboratory tests and woodland spraying with guavas indicate that if there is need for protecting orchard fruits, protection can be obtained by spraying with one of several chemicals found to be toxic to the fly, such as parathion, DDT, and EPN.

SUMMARY

The three species of tephritid fruit flies that are pests in Hawaii are discussed from the standpoint of their economic importance, habits, and control.

These flies are economically important to Hawaii not only because of the damage they do to fruits but also because their occurrence here makes it necessary to have a quarantine against the shipment of untreated fresh fruits to mainland markets.

The habits of the flies in regard to oviposition, food, and shelter have been studied and the information obtained has been especially helpful in the development of effective control measures against the melon fly.

Only partial success has been obtained through the introduction of parasites and predators of these flies, even though much intensive work was done along this line. The biological control approach has been more successful with *C. capitata* and *D. dorsalis* than with *D. cucurbitae.*

Insecticides such as DDT, parathion, and EPN are effective as space and residual sprays; however, spraying of the crop alone has usually given inadequate protection of the crop. Excellent control has been obtained of both *C. capitata* and *D. cucurbitae* by applying the above materials to the vegetation on which the flies are found.

LITERATURE CITED

BACK, E. A. and C. E. PEMBERTON. 1917. The melon fly in Hawaii. *U.S. Dept. Agr. Bull.*, 491: 1-64.

——————. 1918. The melon fly. *U.S. Dept. Agr. Bull.*, 643: 1-31.

BESS, H. A. 1953. Status of *Ceratitis capitata* in Hawaii following the introduction of *Dacus dorsalis* and its parasites. *Proc. Haw. Ent. Soc.*, 15(1): 221-234.

BESS, H. A., ROBERT VAN DEN BOSCH and FRANK HARAMOTO. 1950. Progress and status of two recently introduced parasites of the oriental fruit fly, *Dacus dorsalis* Hendel, in Hawaii. *Proc. Haw. Ent. Soc.*, 14(1): 29-33.

BIRD, K. M. 1952. Summary of legal restrictions affecting trade in Hawaiian Agricultural Products. Agr. Econ. Rept. No. 12. Univ. Haw. Agr. Expt. Sta. in cooperation with the Agr. Expt. Sta. of the western states, and the U.S. Dept. Agr.

CARTER, WALTER. 1950. The oriental fruit fly: Progress on research. *Jour. Econ. Ent.*, 43(5): 677-683.

CLARK, B. O. 1898. Official bulletin of the Bureau of Agriculture. *The Hawaiian*, 1:6.

COQUILLETT, D. W. 1899. A new trypetid from Hawaii. *Ent. News*, 10: 129-130

EBELING, WALTER, T. NISHIDA and H. A. BESS. 1953. Field experiments on the control of the melon fly, *Dacus cucurbitae*. *Hilgardia*, 21: 563-92.

FULLAWAY, D. T. 1919. Control of the melon fly in Hawaii by a parasite introduced from India. *Rept. Proc. 3rd Ent. Meeting, Pusa.*, Feb. 1919: 625-629.

HOLDAWAY, F. G., O. C. MCBRIDE, Y. TANADA and T. NISHIDA. 1947. Progress in the control of the melon fly. *Haw. Agr. Expt. Sta. Rept.*, 1944-46: 61-64.

HOWARD, L. O. 1900. A dipterous enemy of cucurbits in the Hawaiian Islands. *U.S. Dept. Agr. Bur. Ent. Bull. N.S.*, 22: 93-94.

SPIDERS IN SAMOA AND THE SOUTHWEST PACIFIC

By B. J. Marples
Department of Zoology
University of Otago
New Zealand

The spider fauna of Samoa is probably the best known of any in the Southwest Pacific area. Practically all the collecting has been done on the island of Upolu, which measures 45 x 15 miles and has a central ridge exceeding 2000 ft. in height covered with forest. In 1929 Berland described an extensive collection made by Buxton and Hopkins and added 13 species to the 69 already recorded. The present author has made two trips devoted to collecting spiders, the results of which are not yet published, but they will bring the total number of recorded species to 124. These various collections are of some interest in trying to evaluate the comparisons between the faunas of different islands and the attempts to deduce their origins. Seldom if ever can the collector have been concentrating on spiders alone over a considerable period. The present author's first visit, in 1945–46, was of about 12 weeks; the second, in 1950–51, was of 8 weeks. On the first occasion 67 species were found and on the second 73, in spite of the shorter time, and the weather and the localities visited being less favourable. Seventeen species were collected in 1945–46 which were not found again and were found in 1950–51 but not on the first visit. These figures show the value of experience in collecting, while the importance of concentrating is shown by the fact that 41 species were new records for Samoa, 32 of them being new species. Many are small and easily overlooked. Representatives of 8 families not previously recorded were found, one being a new family and others not known from the Southwest Pacific area before.

Berland (1934 and elsewhere) has discussed the distribution of spiders in the Pacific, and lists the species from the different islands. In the light of what is now known of Samoa it seems certain that many more species remain to be recorded, probably even in the low coral islands where the fauna is small. Berland lists, for example, 42 species from Fiji where there are islands larger than any in Samoa, and 160 from New Caledonia, larger still and nearer to continental land. One would imagine that both have a far larger fauna than Samoa, and its list seems by no means complete at 124 species.

Some smaller collections, the descriptions of which are still unpublished, are available from some other islands in the area. The most notable of these are from atolls, the Tokelau Islands with 12 species, and Pukapuka Island in the northern Cook Group with 8 species. No spiders have been recorded from these islands previously and all the species are known also from Samoa. A slight amount of collecting also served to raise the total recorded species of Rarotonga from 5 to 14 and of Tongatabu from 20 to 31.

Of the new records from Samoa perhaps the most notable is *Idioctis helva,* a mygalomorph spider of the family Barychelidae previously known from Fiji. Mygalomorph spiders are usually regarded as confined to continental lands. However, as it occurs close to high water mark on the sea shore in a tough silken tube, its chances of transport by natural raft or accidentally by canoe are reasonably great. Other interesting families are the Symphytognathidae with a species in Samoa and another in Fiji (Marples 1951), and the Archaeidae with one species in Samoa. Two new genera and species of Ochyroceratidae are being described from Samoa. They occur also in Fiji and one, curiously enough, on one of the Tokelau atolls. None of these families seem to have been found previously within the area, and the same is true of the arachnid orders Palpigradi and Schizomi, representatives of both of which occur in Samoa. All these are small and obscure forms not found without careful search.

It is possible that some of these animals have been introduced accidentally by man in the 20 years since Buxton and Hopkins made their collection. A probable example of this is *Filistata bakeri* first recorded in 1945 and which had become abundant in 1950. This explanation, however, is inadequate for most of the examples and it seems certain that, apart from some conspicuous families such as the Salticidae, it is still premature to attempt to compare spider faunas as a whole in the Southwest Pacific. Much more intensive specialised collecting is needed.

REFERENCES

BERLAND, L. 1929. Araignées, in Insects of Samoa and other Samoan terrestrial Arthropoda. Part VIII (2) pp. 35-78. *Brit. Mus. Nat. Hist.* London.

———— 1934. Les Araignées du Pacifique, in Contributions à l'étude du peuplement zoologique et botanique des îles du Pacifique. *Publ. Soc. biogéogr.*, 4. pp. 155-180.

MARPLES, B. J. 1951. Pacific Symphytognathid Spiders. *Pacific Science*, 5. pp. 47-51.

MARINE WOOD-BORING MOLLUSCA OF THE PHILIPPINES

By Robert C. Miller
California Academy of Sciences
San Francisco, California, U.S.A.

In 1924 and in 1927 this writer called attention to *Martesia striata* Linn. as a wood-boring mollusk extremely destructive to submerged timbers in Philippine waters. In the earlier paper he stated that test blocks submerged four months or longer at Cavite were usually in a crumbling condition, the surface being riddled by small *Martesia,* mostly less than 2 cm. in length. In the same paper he reported the occurrence at Cavite of *Teredo parksi* Bartsch, a species described from Hawaii in 1921.

In 1927 Bartsch listed 16 species of shipworms from Philippine waters, all but two of which he regarded as new. In 1928 Sivickis described 15 additional new species from the Philippines. In 1930 the present author visited Manila and studied the Sivickis types which were then in the Philippine Bureau of Science. Some comments on this study may be in order.

Sivickis did not designate type specimens, but based his descriptions on all the specimens he had—sometimes only one, in which case the type is obvious, sometimes up to half a dozen. It is of course desirable to have series, but the best procedure is to designate one specimen as the type, and to describe the range of variation exhibited by the others. This point is now merely academic, since all of Sivickis specimens were destroyed during the war.

Bankia globosa we are convinced is simply a younger and smaller *Bankia quadrangularis.* The pallets are much more alike than Sivickis' photographs show, and there was one extra, smaller pallet in the *B. quadrangularis* bottle that seems intermediate between the two. Since *B. quadrangularis* is described earlier, in the paper, it is the name that should stand.

It is likely that one or two other species of *Bankia* described by Sivickis will ultimately fall into the synonymy, but it is almost impossible to be sure without having the specimens of Bartsch and Sivickis side by side, or else accurate, large photographs of them.

Teredo bartschi Sivickis appears to be a valid species, but the name is preoccupied by *Teredo bartschi* Clapp (1923). We offer therefore as a substitute name *Teredo sivickisi.*

The pallets of this species, which are quite characteristic, are inadequately described by Sivickis. They are deeply cupped, with the outer margin considerably excavated to form a crescent which is narrowly bordered with brown periostracum. The inner margin is characterized by two very shallow excavations, separated by a ridge which is more or less distinctly grooved in the middle. Sivickis' reference to this as a "poorly developed knob in the proximal edge of the cup" is unsatisfactory. There is a groove in the middle of the "knob," which is not a knob but a ridge.

Sivickis' Figure 12, which he identifies only as *Teredo* sp., is pretty obviously also the same thing, in a slightly larger and older version. In my notes I wrote:

"After examining the pallet, I would refer it to the same species. In this and in *bartschi* (sic), the siphons are subequal in length, both fringed and divided to the collar. (It should be explained that in some shipworms the siphons are united for a greater or lesser part of their length). Figure 12 is simply a much larger specimen."

We have not examined Bartsch's types, with the exception of that of *T. mindanensis,* which is different from anything we have seen and appears to be a valid species. We have therefore to accept Bartsch's species, although we must admit that this is slightly unfair to Sivickis, whose types we have inspected with a critical eye. In the list of Philippine wood-boring mollusca that we append, we admit there are likely to be some synonyms; there appears to be no way to correct this except through a world-wide revision of the whole group by some competent authority. We include *Teredo dubia,* which is not a wood-boring species but lives in sand, and should perhaps be assigned to the genus *Kuphus.*

Martesia striata Linnaeus
Bactronophorous edulis Sivickis
Bactronophorous fileoti Sivickis
Bankia philippinensis Bartsch
Bankia johnsoni Bartsch
Bankia barthelowi Bartsch
Bankia davoensis Bartsch
Bankia triangularis Sivickis
Bankia oryzaformis Sivickis
Bankia quadrangularis Sivickis
Bankia tenuis Sivickis
Bankia rubra Sivickis
Eoteredo philippinensis Bartsch
Teredo mindanensis Bartsch
Teredo smithi Bartsch
Teredo radcliffei Bartsch
Teredo tanonensis Bartsch

Teredo macocotana Bartsch
Teredo chamberlaini Bartsch
Teredo pujadana Bartsch
Teredo linaoana Bartsch
Teredo escareoana Bartsch
Teredo mindoroana Bartsch
Teredo luzonensis Bartsch
Teredo variegata Sivickis
Teredo princesae Sivickis
Teredo sivickisi Miller
Teredo dubia Sivickis
Teredo hydei Sivickis
Teredo apendiculata Sivickis
Teredo parksi Bartsch

This list of thirty species of Teredinidae in the Philippines, in addition to *Martesia,* seems unrealistic. It is likely that a number of them will be found to be synonyms of species previously described. These organisms are carried about by obvious means, wooden hulls, drifting timber, and the like, and it is to be expected that the same species should turn up here and there in different parts of the world. For example, *Teredo parksi* Bartsch, originally described from Hawaii, has been found to be an important species in the Philippines; and *T. bartschi* Clapp from Florida and *T. fulleri* Clapp from the Virgin Islands both occur in Hawaii (Edmondson, 1942). Nevertheless Edmondson (*op. cit.*), a very careful and conservative taxonomist, has found at least fourteen species of shipworms in Hawaii, six of which he considers to be new.

There is a large field here for someone, not to describe new species but to find out which of the old species are valid. We do not yet know to what extent these organisms are spread ubiquitously around the world in suitable habitats and to what extent they are limited as to locality.

Literature Cited

Bartsch, P., 1921. A new classification of shipworms and descriptions of some new wood-boring mollusks. *Proc. Biol. Soc., Wash.*, vol. 34, pp. 25-32.

———. 1927. The shipworms of the Philippine Islands. *U.S.N.M. Bulletin* 100, vol. 2, pp. 531-544, pls. 53-60.

Edmonson, C. H., 1942. Teredinidae of Hawaii. Occasional Papers of Bernice P. Bishop Museum, vol. 17, pp. 97-150.

Miller, R. C., 1924. Wood-boring mollusks from the Hawaiian, Samoan, and Philippine Islands. *Univ. Calif. Publ. Zool.*, vol. 26, pp. 145-158, pls. 8-11.

———. 1927, *in* Hill and Kofoid, Marine Borers and their Relation to Marine Construction on the Pacific Coast. Final Report of the San Francisco Bay Marine Piling Committee. 357 pp.

Sivickis, P. B., 1928. New Philippine shipworms. *Philippine Jour. of Science*, vol. 37, pp. 285-298, pls. 1-3.

SPIDER PREDATORS OF THE SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA* (CLEM.), AT LILLOOET, B. C., CANADA[1]

By A. L. Turnbull[2]
Biological Control Section, Entomology Laboratory
University of British Columbia
Vancouver, B. C., Canada

Introduction

Since 1943 an infestation of the spruce budworm, *Choristoneura fumiferana* (Clem.), near Lillooet, Britih Columbia, has been used as a source of insect parasites for shipment to areas in Eastern Canada infested by the budworm (Coppel, 1947; Wilkes, 1947). A number of distinct population foci exist in the area. A close check has been maintained upon some of these foci for 10 years and the population level has varied only slightly until 1953, when it decreased markedly. The only apparent change until 1953 was a slight movement of the population foci, generally from lower to higher altitudes.

Periods of abundance and scarcity in this area have existed for some time. Mr. A. W. A. Phair, who has lived for over 60 years in the village of Lillooet, has distinct recollections of spruce budworm populations of varying numerical abundance in the same general areas throughout that period. Tothill (1923) reported on an outbreak in 1919 and the factors responsible for its reduction.

The vast potential of this subepidemic population of the spruce budworm is obvious, yet the insect has never become sufficiently abundant anywhere in the region to cause tree mortality. It is apparent that an efficient natural control complex is operating in the area that prohibits the increase of the spruce budworm population to epidemic levels. The region, therefore, is eminently suitable for the study of the interrelations between the spruce budworm and the control complex.

Spiders abound in the budworm-infested forest, and some species were observed capturing spruce budworm larvae and moths. Preliminary feeding tests in 1949 and 1950 demonstrated that some spiders accepted spruce budworm larvae and moths as food. This is a report on the effect of predation by spiders on the budworm population.

---

[1] Contribution No. 3171, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

[2] Agricultural Research Officer.

METHODS

Determination of Spider Fauna

Qualitative

Only species of spiders taken from the foliage of Douglas fir, *Pseudotsuga taxifolia* (Poir.) Britton, in the budworm-infested area were considered. Specimens were taken by individual capture, by beating foliage into an umbrella, by sweeping foliage, and by applying a lethal spray.

1. Individual capture yielded the most information on the specimens captured, but yielded a disproportionate number of the more conspicuous species.

2. Beating foliage into an umbrella was very successful. The abundance of many inconspicuous, vagrant species first became apparent by the use of this method, but detailed observations on specimens were lacking.

3. Sweeping foliage with a long-handled nylon net proved unsatisfactory. Only branch tips could be swept. The method yielded no species not obtained by beating, and was more difficult to employ.

4. A lethal spray, Cypro-emulsion Concentrate (Commercial Chemicals Limited, Vancouver, B. C.), an oil-based emulsion containing 1.18 per cent pyrethrins and 11.8 per cent piperonyl butoxide, was efficient and fast-acting. A solution of one part to five parts of water was employed. A back-pack, hand-operated pump was used to apply the spray.

One day in advance, small shrubbery and herbaceous plants were removed from within 15 feet of each tree to be sprayed. The area beneath the canopy, and four to five feet beyond, was covered with cotton sheets. On the following day the sheets were thoroughly sprayed. The tree was then sprayed quickly, starting at the apex and working down. Repeated observations indicated that the entire fauna of the tree was incapacitated within 10 minutes, but a 15-minute interval was allowed before material was collected. At the end of this period the crown of the tree was thoroughly beaten with a pole to ensure that no specimens remained adhering to the foliage. All collected material was placed immediately in individual vials containing 80 per cent alcohol.

Quantitative

Quantitative samples were obtained by the lethal-spray method. Two experimental areas were used, one within a population focus (Plot A) and one outside population foci (Plot B). No area otherwise similar to Plot A could be found that was free of the spruce budworm;

however, an area was located 15 miles distant where the budworm population was small and other factors similar.

The experimental areas each comprised were about 10 acres of 10- to 30-year-old Douglas fir forest. The trees were widely spaced, and the forest canopy was never closed. Deciduous trees and shrubs such as cottonwood, aspen, saskatoon, and chokecherry occupied about 20 per cent of the ground. There were many grassy openings between clumps of trees.

The sample unit employed was an individual tree. As the maximum height to which the hand-pump could deliver spray was 17 feet, only trees 15 feet and under were selected. Also, trees were selected that, though not isolated from the surrounding forest, stood more or less alone so that the fauna from overhanging boughs of adjacent trees would not fall on the mats.

There were 49 trees suitable for sampling in Plot A and 38 in Plot. B. These were marked by numbered tags. Two trees from each plot were chosen by lot every week from June 1 to August 24 for sampling.

The first samples were taken on June 1, 1951, when most of the spruce budworm were in the third instar, although individuals of the second instar were still numerous, and a few fourth-instar larvae were to be found. The tree buds were well opened but still bore the bud caps.

Field Observations

Observations of spiders in their natural environment yielded many details on the capture of the spruce budworm by spiders, vulnerable stages of the budworm, methods of capture, and methods of their defence against capture.

Feeding Tests with Captive Spiders

Melrose boxes, 6 by 8½ by 2½ inches, were used to cage web-spinning species. The bottom of the box was covered with blotting paper, which was allowed to protrude an inch beyond one edge of the box. A few drops of water applied daily to the exposed paper provided sufficient moisture. Two one-inch holes were drilled in each end of the box. Three of these were covered with gauze. The fourth hole was stoppered with a cork and was used for inserting and removing the insects used as food.

Vagrant spiders were kept in 90-mm. petri dishes. A sheet of blotting paper was cut to fit snugly into the larger part of the dish. This part was used as the base, and the smaller part was inverted into it.

The blotting paper was moistened daily by placing a drop of water between the two parts.

To prevent cannibalism each cage held only one spider. Spiders were fed only one insect per feeding. In each case insects not captured by the spider were removed from the cage at the next feeding and a new insect provided. The number of spiders of each species tested varied with the number available at the time of the tests. Four series of tests were conducted, three with various flies as food (Series A, B, and C), and one with spruce budworm larvae (Series D).

Series A.—Three species of spiders were tested using drosophila flies as food. The species and numbers of spiders tested were: *Parasteatoda tepidariorum* (Koch), 12; *Metaphidippus flavipedes* (Peck.), 8; *Aranea displicata* (Hentz), 5. Spiders were fed thrice daily except Saturdays and Sundays at 9.00 a.m., 12.00 noon, and 4.30 p.m.; on Saturday they were fed at 9.00 a.m. and 12.00 noon; on Sundays they were not fed. A record of consumption was kept for six weeks.

Series B.—Cluster flies (Family Calliphoridae, probably *Nitellia* sp.) were used as food. The species and numbers of spiders tested were: *P. tepidariorum,* 8; *M. flavipedes,* 3; *A. displicata,* 4. The living flies were weighed before being placed in the cages, and the cadavers of the consumed flies were weighed after they were discarded by the spiders. Feeding times were 9.00 a.m. and 4.30 p.m. except on Saturdays, when the second feeding was at 12.30 p.m., and on Sundays, when the spiders were not fed. A record of consumption was kept for four weeks.

Series C.—The common house fly, *Musca domestica* L., was used as food. The species and numbers of the spiders tested were: *M. flavipedes,* 10; *Paraphidippus marginatus* (Walck.), 6; *Evarcha hoyi* (Peck.), 8; *Philodromus rufus* Walck., 7; *Xysticus punctatus* Keys., 10; *Thanatus* sp., 6; *Allotheridion murmarium* (Emerton), 4; *Allotheridion differens* (Emerton), 5; *Aranea gemmoides* Chamb. & Ivie, 8; *Cyclosa conica* (Pallas), 6. Records were kept for three weeks. Spiders were fed twice daily, at 9.00 a.m. and 8.00 p.m., including Saturdays and Sundays.

Series D.—Spruce budworm larvae were used as food. The species and numbers of spiders tested were: *M. flavipedes,* 6; *P. marginatus,* 4; *E. hoyi,* 4; *P. rufus,* 5; *X. punctatus,* 5; *Thanatus sp.,* 3; *A. murmarium,* 2; *A. differens,* 2; *A. gemmoides,* 4; *C. conica,* 6. Larvae were provided thrice daily at 9.00 a.m., 1.00 p.m., and 8.00 p.m. Records were kept for three weeks.

Several difficulties arose when these larvae were fed to web-spinning spiders. Unless introduced directly into the spider's web, the larva, crawling on the sides of the cage, would encounter only anchor lines of the web and might never become ensnared. The violent vibrations set up in the web lines by the artificial introduction of a larva alarmed the spider, often causing it to abandon the web, and the larva was able to escape.

The different growth rates of the spider and its prey further complicated these tests. The spruce budworm larvae passed from the third to the sixth instar during the test period, many of them almost tripling in size. The healthiest spider moulted only once, and none doubled in size. Consequently, a spider that at the start of the tests could consume three third-instar larvae per day was unable at the end of the tests to capture a single fifth-instar larva, or had reduced its consumption to not more than one larva every two or three days.

Analyses of Cadavers in Spider Webs

Many spiders dispose of the cadavers of their victims by hanging them in their webs, or by dropping them to the substratum. In the summer of 1951 the accumulated cadavers of 50 argiopid (species not determined) spider webs were collected. Most of the cadavers were heavily swathed in silk and were in various stages of mutilation and decomposition. Most of them were determined to order with reasonable accuracy, but further naming was of doubtful validity. The cadavers of spruce budworm larvae were easily distinguished by means of the head capsule, which was usually unmutilated. Essentially the same procedure was used by Exline and Hatch (1934) and Pratt and Hatch (1938) to determine the prey of the black widow spider.

RESULTS

Determination of the Spider Fauna

Qualitative

A list of the spiders taken from Plot A is given in Table I. All of the abundant species are included. Many of the species listed are probably only incidental visitors to coniferous foliage and do not contribute to spruce budworm mortality.

TABLE I

SPECIES OF SPIDERS FOUND IN DOUGLAS FIR FOREST INFESTED BY THE SPRUCE BUDWORM, WITH MONTHS OF COLLECTIONS, LILLOOET, B.C., 1951, 1952.

SPECIES	COLLECTION MONTH
Pholcidae C. L. Koch	
Pholcophora americana Banks	Aug., 1951
Theridiidae Sundevall	
Allotheridion differens (Emerton)	June, 1951

TABLE I (Continued)

Species	Collection Month
Allotheridion murmarium (Emerton)	June–September, 1951
Allotheridion neomexicanum (Banks)	July, 1951
Allotheridion ohlerti Thorell	June, 1951
Dipoena sp.	June, 1951
Euryopsis formosa Banks	June, 1951
Latrodectus mactans (Fabr.)	August, 1951
Steatoda hespera Chamb. & Ivie	July, 1951
Theridion wyutum Chamb. & Ivie	July, 1952
Linyphiidae Blackwall	
Linyphia marginata C. L. Koch	July, 1950
Linyphia litigiosa Keys.	September, 1951
Pityohyphantes cristatus Chamb. & Ivie	June, 1952
Pityohyphantes minidoka Chamb. & Ivie	July, 1952
Pityohyphantes kamela Chamb. & Ivie	June, 1951
Pityohyphantes brachygynus Chamb. & Ivie	July, 1951
Micryphantidae Bertkau	
Ceratinella placida Banks	June, 1951
Argiopidae Simon	
Aranea displicata (Hentz)	July, 1951
Aranea gemmoides Chamb. & Ivie	June, 1951
Aranea patagiata Clerck	May–June, 1951
Aranea solitaria (Emerton)	July, 1951
Calymmaria monicae Chamb. & Ivie	July, 1952
Cyclosa conica (Pallas)	May–August, 1951
Tetragnathidae Menge	
Tetragnatha versicolor Walck.	August, 1951
Agelenidae C. L. Koch	
Agelenopsis utahana (Chamb. & Ivie)	September, 1951
Agelenopsis potteri (Blackwall)	August, 1951
Agelenopsis idahoana Chamb.	May, 1952
Tegenaria gigantea Chamb & Ivie	July, 1950
Hahniidae Bertkau	
Neoantistea gosiuta Gertsch	August, 1951
Lycosidae Sundevall	
Lycosa frondicola Emerton	September, 1952
Lycosa avida Walck.	June, 1951
Pardosa mackenziana (Keys.)	June–September, 1951
Pardosa tristis Thorell	July, 1951
Pardosa vancouveri Emerton	August, 1950
Tarentula aculeata (Clerck)	August, 1952
Oxyopidae Thorell	
Oxyopes rufipes Banks	June, 1951
Oxyopes scalaris Hentz	July, 1951
Gnaphosidae Pocock	
Drassodes neglectus (Keys.)	June–August, 1951
Gnaphosa muscorum (L. Koch)	May–August, 1951
Poecilochroa montana Emerton	July–August, 1952

TABLE I (Continued)

Species	Collection Month
Zelotes puritanus Chamb.	September, June, 1951
Clubionidae Wagner	
Anyphaena pacifica (Banks)	June, 1951
Castianeira descripta (Hentz)	July, 1951
Clubiona emertoni Petrunkevitch	July, 1951
Phrurotimpus parallelus Chamb.	July, 1952
Thomisidae Sundevall	
Coriarachne utahensis (Gertsch)	July, 1951
Misumena vatia (Clerck)	August, 1951
Misumenops celer (Hentz)	August, 1951
Philodromus aureolus Clerck	June, 1951
Philodromus pacificus Banks	August, 1952
Philodromus praelustris Keys.	July, 1951
Philodromus nr. *rodecki* (n. sp.?)	July, 1951
Philodromus rufus Walck.	June–September, 1951
Philodromus speciosus Gertsch	September, 1952
Thanatus sp.	July, 1952
Tmarus angulatus (Walck.)	September, 1951
Xysticus elegans Keys.	June–September, 1951
Xysticus malkini Gertsch	July, 1951
Xysticus punctatus Keys.	July, 1951
Xysticus pulverulentus Gertsch	June, 1951
Xysticus triangulosus Emerton	June, 1951
Xysticus locuples Keys.	July, 1950
Salticidae Blackwall	
Evarcha hoyi (Peckham)	September, June, 1951
Habronatus sp.	June–August, 1951
Metaphidippus aeneolus Curtis	July, 1951
Metaphidippus flavipedes (Peckham)	June–July, 1951
Metaphidippus vitus Cockerell	July, 1951
Paraphidippus marginatus (Walck.)	June–August, 1951
Phidippus formosus Peckham	June–July, 1951
Dictynidae Cambridge	
Callobius serverus Simon	July–August, 1951
Callobius pictus Simon	July–August, 1951
Dictyna brevitarsis Emerton	June–September, 1951
Dictyna phylax Gertsch & Ivie	July, 1952
Mallos alpheus Chamb.	June, 1952
Uloboridae Cambridge	
Hyptiotes gertschi Chamb. & Ivie	June, 1952

Quantitative

Table II shows the total number of spiders of each family obtained by sampling trees in Plots A and B. Of 330 spiders from the 14 families represented, 35.5 per cent were Salticidae and 33.7 per cent were Thomisidae. Of the remaining families, only the Argiopidae and the

Theridiidae were sufficiently abundant to contribute significantly to spruce budworm mortality.

TABLE II

Numbers of Spiders of Various Families Obtained When the Complete Fauna Was Removed from 26 Douglas Fir, *Pseudotsuga taxifolia* (Poir.) Britt., Trees at Lillooet, B.C., 1951, 13 Trees Being in a Spruce Budworm Population Focus (Plot A) and 13 Trees outside Population Foci (Plot B).

Family	Plot A	Plot B
Salticidae	60	57
Thomisidae	47	65
Theridiidae	16	7
Argiopidae	9	7
Dictynidae	10	5
Oxyopidae	4	9
Agelenidae	8	1
Clubionidae	2	6
Linyphiidae	2	6
Gnaphosidae	1	3
Lycosidae	2	0
Hahniidae	1	0
Micryphantidae	0	1
Uloboridae	1	0
Total [a]	163	167

[a] Mean number of spiders per tree: A, 12.54 ± 6.5 (limits of confidence at 1% level); B, 12.84 ± 4.8.

Table III shows the relative abundance of the species comprising the four major families present in the two sample areas. It is apparent that two species, *M. flavipedes* and *P. rufus,* which together contribute one-third of the spider population, are the most abundant spiders on coniferous trees in the Lillooet region.

Analysis of variance indicated no significant difference between the spider populations in Plots A and B (sufficient numbers of specimens for a statistical test were obtained for only three families, the Salticidae, the Thomisidae, and the Theridiidae). Student's *t* test indicated no significant difference between the means of the three families in the two areas.

Field Observations

On May 26, 1951, at 2.30 p.m. the author observed an air-borne dispersal of second-instar spruce budworm larvae. This type of dispersal has been described by Wellington and Henson (1947). Larvae were dropping by means of silken threads from upper to lower branches

TABLE III

RELATIVE ABUNDANCE OF SPECIES OF THE FOUR MAIN SPIDER FAMILIES OCCURRING ON DOUGLAS FIR TREES AT LILLOOET, B.C., MAY-SEPTEMBER, 1951.

SPECIES	NUMBER	PER CENT OF FAMILY	PER CENT OF TOTAL [a]
Salticidae			
M. flavipedes	72	61	21.8
P. marginatus	20	17	6.1
E. hoyi	15	13	4.5
M. aeneolus	6	5	1.8
Habronatus sp.	3	3	0.9
M. vitus	1	1	0.3
Total	117		35.4
Thomisidae			
P. rufus	40	36	12.1
X. punctatus	15	13	4.5
P. speciosus	12	11	3.6
Thanatus sp.	11	10	3.3
P. pacificus	10	9	3.0
T. angulatus	9	8	2.7
X. malkini	6	5	1.8
C. utahensis	5	4	1.5
P. rodecki	2	2	0.6
M. vatia	1	1	0.3
X. pulverulentus	1	1	0.3
Total	112		33.7
Theridiidae			
A. murmarium	6	26	1.8
A. differens	6	26	1.8
Dipoena sp.	6	26	1.8
A. neomexicanum	2	9	0.6
A. ohlerti	2	9	0.6
E. formosa	1	4	0.3
Total	23		6.9
Argiopidae			
A. gemmoides	9	56	2.7
A. displicata	3	19	0.9
C. conica	3	19	0.9
A. diademata	1	6	0.3
Total	16		4.8

[a] Based on total of 330 spiders from Table II.

of trees; others were drifting freely on air currents. Numerous webs of the orb-spinning spider, *A. displicata,* were suspended between the tips of adjacent branches. Thirty-eight of these webs were examined in a two-hour period. Drifting spruce budworm larvae had become entangled in six of them. In some cases the larva had struck the web directly; in others the larva's silken thread became entangled in the spider's web and the larva climbed up the thread to the web. In both cases the spider did not hesitate to attack, and the larvae were quickly subdued. Only a small fraction of the total number of webs in the area was examined. At that time of the year *A. displicata* is in the juvenile stage and builds a delicate web about six inches in diameter. These filmy webs are almost invisible, and are easily overlooked.

In the later feeding stages, spruce budworm larvae often drop on silken lines from the upper to the lower part of the tree (Wellington and Henson, 1947; Wellington, 1948). On such occasions their descent is sometimes intercepted by the network of a spider web. An ensnared larva is usually quickly subdued by the host spider, but occasionally the spider's attack is repelled and the larva escapes.

Spruce budworm larvae do not submit passively to capture by spiders. Their reaction to attack is a violent threshing of the entire body accompanied by the oral exudation of a sticky, brown, evil-smelling liquid. By these tactics larvae of the fourth and later instars can often repel the attack of a spider. If the spider can be prevented from administering the paralyzing venom, a larva can often escape from the web.

Dropping spruce budworm larvae become ensnared in both argiopid and theridiid webs. Although most of the Theridiidae are smaller than the Argiopidae, they have developed a more efficient method of attack, and rarely allow a victim to escape from their webs. The theridiid spiders are equipped with a comb-like apparatus on the fourth tarsi by means of which they can cast a band of swathing silk over their victims from a distance, and thus secure opponents much stronger than themselves. Only after the victim is securely bound does the spider approach and administer the venom. Though the argiopids also bind their prey, they lack the efficiency of the theridiids and often cannot subdue a vigorous opponent with swathing silk or approach close enough to administer the venom.

The theridiid spiders often spin a maze-like tangle of threads over the terminal ends of Douglas fir branches, some of which are inhabited by spruce budworm larvae. When the larvae move about in search of fresh foliage, they inevitably come into contact with the viscid lines of the webs and fall prey to the spiders. On June 8, 1953, 78 such webs were found in a four-hour search of an area about half a mile square. Twenty-three webs were on branch tips not inhabited by the spruce budworm. The buds were unopened on 38 of the infested branches and the larvae were hidden within them. The buds on the remaining 17 branches had opened and the larvae were exposed. Six larvae were feeding normally; seven larvae were entangled in the webs but had not been attacked; and the remaining four larvae had been captured. During the period of observation three additional larvae were attacked.

Salticid spiders were frequently observed capturing spruce budworm larvae. These spiders have no difficulty subduing vigorous sixth-instar larvae. No method was devised for obtaining quantitative data on predation by this family in the field, but their abundance and the frequency with which they were observed feeding on spruce budworm larvae indicated their effectiveness.

Spruce budworm adults are susceptible to predation by both web-spinning and vagrant spiders. During the period of moth flight in 1952 the webs of 39 argiopid and 34 theridiid spiders were examined at night by the light of an electric torch. Practically every web had at least one budworm moth in it, and one had six. Eighty-five moths were found in argiopid webs, and 46 in theridiid webs.

Night observations revealed frequent captures of spruce budworm moths by salticid spiders. Six salticids found feeding on moths were captured in one evening. The moths were all gravid females. Four of the spiders were of *P. marginatus,* and the others were of *E. hoyi.*

Feeding Tests with Captive Spiders

Of the four families of spiders represented in the tests, species of three families accepted spruce budworm larvae as food. The Thomisidae consistently failed to capture budworm larvae, although under similar conditions they captured house flies. Table IV shows the average weekly consumption of insects per spider of each species tested. The fiducial limits indicate the large variation in the daily consumption of spiders of the same species.

Analyses of Cadavers in Spider Webs

One hundred and fifty-two cadavers were found in the webs of 50 argiopid spiders; of these 25.7 per cent were Diptera, 10.5 per cent were Hymenoptera, 9.9 per cent were Lepidoptera, including the spruce budworm, 11.2 per cent were Neuroptera, 1.9 per cent were Megaloptera, 5.3 per cent were Raphidoidae, 18.4 per cent were Trichoptera, and 17.1 per cent were unidentified. Of the lepidopterous cadavers, seven (4.6 per cent of the total) were spruce budworm larvae. It is apparent that the budworm is not a major part of the diet of this spider group.

DISCUSSION

Seventy-five species of spiders representing 15 families were collected from the foliage of Douglas fir trees at Lillooet. Spiders of four

TABLE IV

MEAN NUMBERS OF DROSOPHILA FLIES (SERIES A), CLUSTER FLIES [a] (SERIES B), THE HOUSE FLY (SERIES C), AND SPRUCE BUDWORM LARVAE (SERIES D) CONSUMED PER CAGED SPIDER.

SPECIES OF SPIDERS TESTED	SERIES A		SERIES B			SERIES C		SERIES D	
	No. of Spiders Tested	Mean No. Consumed [b]	No. of Spiders Tested	Mean No. Consumed	Mean Wt. Consumed (mg.)	No. of Spiders Tested	Mean No. Consumed	No. of Spiders Tested	Mean No. Consumed
Salticidae									
Metaphidippus flavipedes	8	2.80±1.54	3	2.17±3.80	26.28±43.57	10	2.83±1.60	6	2.11± 1.09
Paraphidippus marginatus	—		—			6	3.94±2.48	4	2.08± 1.51
Evarcha hoyi	—		—			8	2.58±1.61	4	2.67± 2.83
Thomisidae									
Philodromus rufus	—		—			7	2.09±2.13	5	0.40± 0.32
Xysticus punctatus	—		—			10	2.10±1.12	5	0
Thanatus sp.	—		—			6	2.00±1.67	3	0
Theridiidae									
Parasteatoda tepidariorum	12	6.26±2.48	8	3.56±1.50	39.95±15.34	—		—	
Allotheridon murmarium	—		—			4	1.33±2.89	2	2.67±10.88
Allotheridion differens	—		—			5	2.07±2.05	2	2.50± 6.83
Argiopidae									
Aranea displicata	5	5.00±4.28	4	2.38±1.83	25.72±17.70	—		—	
Aranea gemmoides	—		—			8	3.54±1.59	4	3.67± 1.95
Cyclosa conica	—		—			6	2.78±2.06	6	2.83± 1.70

[a] Probably *Nitellia* sp.
[b] Fiducial limits at 5%

families, the Salticidae, the Thomisidae, the Theridiidae, and the Argiopidae, constituted 80 per cent of the population. Seventy per cent of the population consisted of the Salticidae and the Thomisidae. Present evidence indicates that the Thomisidae do not capture spruce budworm larvae; caged specimens captured spruce budworm moths, but this was not observed in the field. The other three families capture both budworm larvae and moths under natural conditions.

Though the web-building theridiids and argiopids capture spruce budworm larvae, these captures appear to be only incidental additions to their normal diet. Aerial webs are primarily constructed for the capture of flying insects and are normally ineffective for capturing lepidopterous larvae. At certain periods in their lives a few budworm larvae become entangled in these webs, but the effect on the budworm population is not great. Evidence presented indicates the relative importance of budworm in the diet of the argiopid spiders: only 4.6 per cent of the insects found in the webs examined were budworm larvae.

The aerial webs of the Argiopidae and the Theridiidae trap large numbers of spruce budworm moths. Gravid moths of the female spruce budworm are incapable of flight until at least one or two egg masses have been dropped (Wellington and Henson, 1947). It is unlikely, therefore, that any female moths are destroyed by aerial web-spinners before a considerable portion of their eggs has been deposited; consequently, the effect of this type of predation on the budworm population is limited.

Spiders of the family Salticidae constituted over 35 per cent of the total foliage-dwelling population of spiders. The salticids are aggressive hunters that prowl the branches of trees and shrubs in search of prey, and in a spruce-budworm-infested forest they inevitably encounter many budworm larvae. Laboratory tests and field observations showed that the Salticidae readily recognize and accept budworm larvae as food. Members of this family are probably the most important spider predators of spruce budworm larvae.

Spruce budworm moths are also captured by the salticids. The sluggish, fully gravid females are especially vulnerable to the tactics of these hunters. This predation is probably important in holding populations in check.

The numbers of spruce budworm larvae consumed by caged spiders of the families Argiopidae and Theridiidae (Table IV) bear no relation to field consumption. The tests show that these families readily accept budworm larvae as food if the opportunity arises; however, it was observed that under natural conditions budworm larvae are captured by these families in limited numbers and the bulk of their food consists of other insects.

The Salticidae are adapted to the use of spruce budworm larvae as food. Table IV shows the consumption of budworm larvae by the salticids in the absence of any other food. Although it is probable that the salticids capture more of the budworm than any of the other insect species in an infested forest, it is not suggested that other insects are not frequently captured; therefore, the figures in Table IV can be taken only as an approximation of the field consumption of budworm larvae by the salticids.

Population samples indicated a mean of 4.5 salticid spiders per sampled tree at any given time. Feeding tests indicated that the average salticid will consume 2.3 spruce budworm larvae per week. Over the eight-week larval feeding period, therefore, 18.4 larvae might be consumed by each spider, or a total of 83 larvae per tree. Though this calculation is only an approximation, it probably errs on the conservative side. The average consumption of budworm larvae per spider in the feeding tests was decreased by the inclusion of injured and nonvigorous spiders; and the trees employed in the population study did not exceed 15 feet in height, whereas the mean height of trees in the area was 36 ± 11.9 feet, more than twice the size of the sampled trees.

SUMMARY

Seventy-five species of spiders representing 15 families were collected from the foliage of Douglas fir trees near Lillooet, British Columbia. Twenty-seven species comprised 80 per cent of the population and represented only four families, the Argiopidae, the Theridiidae, the Thomisidae, and the Salticidae. The families Thomisidae and Salticidae represented 69.4 per cent of the population, 33.7 per cent being thomisids and 35.5 per cent being salticids.

The thomisids, although very abundant, did not capture spruce budworm larvae or moths. The argiopids and theridiids capture spruce budworm larvae if the opportunity arises, but these opportunities occur only occasionally. These families do capture large numbers of spruce budworm moths, though it is probable that female moths drop at least a portion of their eggs before they are destroyed.

The salticids readily accept budworm larvae as food, and are well equipped to capture this type of prey. Members of this family also capture budworm moths. The majority of these captures probably occur before the female moths begin oviposition. The salticids probably exert a restraining influence on spruce budworm populations in the Lillooet district.

ACKNOWLEDGMENTS

All the spiders used in this study were determined by Dr. W. J. Gertsch of the American Museum of Natural History, New York. In addition, the writer is indebted to Dr. Gertsch for valuable instruction on the taxonomy of spiders.

REFERENCES

COPPEL, H. C. (1947): The Collection of Spruce Budworm Parasites in British Columbia with Notes on Their Overwintering Habits. *77th Ann. Rept. Ent. Soc. Ontario*, 1946, 38-40.

EXLINE, H. and M. H. HATCH. (1934): Note on the Food of the Black Widow Spider. *J. New York Ent. Soc.*, 42, 449-450.

PRATT, R. Y. and M. H. HATCH. (1938): The Food of the Black Widow Spider on Whidley Island, Washington. *J. New York Ent. Soc.*, 46, 191-193.

TOTHILL, J. D. (1923): Notes on the Outbreak of Spruce Budworm, Forest Tent Caterpillar and Larch Sawfly in New Brunswick. *Proc. Acadian Ent. Soc.*, 8, 172-182.

WELLINGTON, W. G. and W. R. HENSON. (1947): Notes on the Effects of Physical Factors on the Spruce Budworm, *Choristoneura fumiferana* (Clem.). *Canadian Ent.*, 79, 168-170.

WELLINGTON, W. G. (1948): The Light Reactions of the Spruce Budworm, *Choristoneura fumiferana* (Clem.). *Canadian Ent.*, 80, 56-82.

WILKES, A. (1947): The Introduction of Insect Parasites of the Spruce Budworm, *Archips fumiferana* Clem., into Eastern Canada. *Canadian Ent.*, 78, 82-86.

THE GUITARFISHES, FAMILY RHINOBATIDAE, OF THE PHILIPPINES AND ADJACENT SEAS

By Albert W. C. T. Herre
School of Fisheries, University of Washington
Seattle 5, Washington, U.S.A.

The guitarfishes are large to very large rays found along all Philippine coasts. Their size and appearance make them of interest to the general public, and their economic value makes them worthy of consideration, but their mode of living and habits prevent them from being well known to most people. They form the natural family Rhinobatidae, composed of large shark-like rays found in all seas except those of arctic and subarctic waters.

The Rhinobatidae are long large-headed fishes with a depressed and somewhat shark-like body. Like all the other rays, the body is wider and flatter than in any of the sharks, and is more or less disclike anteriorly. The pectoral fins are widened and enlarged to form the sides of the disk, which passes gradually into the long, strong, depressed tail. The pectorals never extend forward beyond the sides of the head or to the tip of the snout, which is more or less extended. There is a conspicuous fold of skin along each side of the tail. The numerous small teeth form a pavement, adapted to crushing the Crustacea and Mollusca which form their principal food. The large eye has a projecting shield. Spiracle large, close to eye. The large oblique nostrils are of characteristic shape in each genus and there are no grooves connecting the nostrils and mouth. Two high pointed dorsal fins. Caudal fin well developed, of small to medium size, sometimes lunate. The scaled body is generally smooth, but warty or bony tubercles or spines may be present on the back and shoulders and about the eyes and spiracles. Of the nine genera recognized by Norman in his monograph, three are found in the Philippines.

Guitarfishes live on the sandy or muddy bottom of bays, harbors, estuaries, and quiet seas without strong currents. They are found at all depths, from a couple of meters down to 150 meters or more. They feed upon shrimp, crabs, and other Crustacea, various small mollusks, and on small fishes. They are often caught with hook and line and some species are desperate fighters, giving the angler a hard struggle. Large ones are prone to break the tackle and escape. In some regions they are eagerly sought by anglers who wish to catch a fish that will test their skill and strength. They are fished for on the bottom, from wharfs, or pantalands, docks or breakwaters, and from boats. They are also taken by seining and are often caught in fish corrals or baklad, and in fish traps, or bobos. In recent years many have been taken by both beam and otter trawlers in bays, gulfs, and the open sea. The development of trawling in the Philippines has not only revealed the presence of guitarfish where they had not been taken before, and of species hitherto unknown in our waters, but has shown them to be more abundant than formerly supposed.

In color they are all more or less gray, varying to dull brown or bluish gray, the under surface white or whitish. Some kinds are more variegated, having small spots or rings scattered over the upper surface, each enclosing a black spot; others have ocelli or eye-like spots or white with black spots and bars. With age the spots tend to disappear.

KEY TO THE GENERA OF PHILIPPINE RHINOBATIDAE

A. Origin of the first dorsal over the ventrals, which are considerably behind the pectorals; pectorals do not extend forward beyond the mouth; a well developed subcaudal fin . . .

B. Snout narrow, elongate; mouth not waved; nostril length about equal to distance between the nostrils; spiracles with two folds on their hind margins .... RHYNCHOBATUS

BB. Snout very broad and rounded; mouth arched forward and deeply waved; nostril length less than distance between the nostrils; spiracles without folds .... RHINA

AA. Origin of the first dorsal well behind the ventrals, which are close to the pectorals; subcaudal indistinct and little developed; pectorals extend forward beyond the mouth but not upon the snout; nostrils oblique; spiracles with one or two folds .... RHINOBATOS

Genus RHYNCHOBATUS

Rhynchobatus

MÜLLER and HENLE, *Sits. Ber. Akad. Wis.* Berlin, p. 16, 1837; type *Rhinobatus laevis* Bl. & Schn.

GARMAN, *Mem. Mus. Comp. Zool.*, vol. 36, p. 268, 1913.

FOWLER, *Bull. 100, U.S. National Mus.*, vol. 13, p. 300, 1941.

Rhynchobatis

MÜLLER and HENLE, *Syst. Beschr. Plagiostomen*, p. 111, 1841; type *Rhinobatus laevis* Bloch and Schneider.

The members of this genus are large to very large rays of the western Pacific and Indian Oceans, and the west coast of Africa. Of the three species recognized, only one is widely distributed and occurs in Philippine waters.

SHOULDER-SPOT GUITARFISH
ARADO — PATING SODSOD
Rhynchobatus djiddensis (Forskal)

The commonest guitarfish in Philippine and adjacent seas is the shovell-nose, or white-spotted, guitarfish (*Rhynchobatus djiddensis*). It is the pating sodsod of Manila Bay and much of Luzon. The Ilocanos know it as immaradu, and it is arado to most Bikolanos, while others call it robarob. The usual Visayan name is bariwan, but it is sorsor in the Banton dialect. The Kuyanos call it kamansi-an and paitan.

The pating sodsod reaches a length of three meters and a weight of more than 225 kilos, but the largest Philippine specimens I have seen were about two and a half meters long and weighed between 75 and a hundred kilos. This fish is often seen in fish markets throughout the Philippines, from Aparri to Sitankai, though it is rare to see one for sale more than a meter in length. The flesh is of excellent quality and is eaten both fresh and dried. The oil of the liver is much esteemed in some regions. The dorsal fins are dried for the Chinese trade and make a fine quality of shark's fin soup.

The elongate narrow snout is contained four to five times in the total length, excluding the caudal fin, and is proportionally shorter in adults than in the young. The head is 2.25 to 2.8 times in the length. The snout is about 1.6 times in the head, the eye 9.5 to 10.5 times and about 7 times in the snout. The teeth are in 40 to 42 rows in each jaw in small specimens; Garman gives 63 rows in the upper jaw of a large specimen. The nostrils are large, oblique, their length equal to the distance between their lower or inner ends, and three-fourths of the width of the mouth, each nostril with a short lobe on its upper or anterior valve. The spiracles nearly equal the eyes, and are close behind them, each with two folds on the hind margin. The origin of the first dorsal is over that of the ventrals and somewhat distant from the pectorals; the second dorsal is nearer the caudal than the origin of the first dorsal. As in all the guitarfishes the body and depressed tail merge imperceptibly behind the pectorals, with a small dermal keel on each side of the tail, its origin above the end of the ventrals.

There is a row of small spines or tubercles over the backbone, two short rows on each shoulder, the inner row larger, a row above each eye from the front margin around to the spiracle above the inner orbital margin.

The arado is a gray fish, its body sprinkled with small white spots; over each shoulder girdle there is a black or dark brown spot equal to or smaller than the eye, and surrounded by a ring of white spots. The under side is more or less whitish to gray. Some large specimens are said to become grayish brown, but all I have seen had the characteristic markings.

The shovel-nose is a famous angling fish, its size, strength, and fighting spirit making it prized by sport fishermen of the Indian Ocean and east coast of Africa. Few anglers are able to land a large specimen. To Philippine anglers seeking new thrills I suggest going after this fish, using meat or fish for bait. Favorable localities would be the Sitankai area, Malampaya Sound, Ragay Gulf, the entrance to Manila Bay, and the China Sea from Fortune Island to Subic Bay.

From the Philippines and East Indies it is found north to Japan, east and south to New Guinea and the Louisade Archipelago, and tropical Australia; it is on the coast of Indo-China and from Malaya extends to Ceylon, India, the Red Sea, and the whole east coast of Africa as far south as Natal.

Genus RHINA Bloch and Schneider

Rhina

Bloch and Schneider, *Syst. Ichth.*, p. 352, 1801. Type *Rhina ancylostomus* Bl. and Schn.

Fowler, *Bull. 100, U.S. Nat. Mus.*, vol. 13, p. 298, 1941.

Rhamphobatis

Gill, *Ann. Lyceum Nat. Hist.* New York, vol. 7, p. 407, 1861; type *Rhina ancylostoma* (Bl. & Schn.)

Garman, *Memoirs Mus. Comparative Zool.*, vol. 36, p. 267, 1913.

The chief features of this genus are the short, broad, bluntly rounded snout and the deeply waved mouth, which is arched forward. Spiracles large, without folds, the nostrils nearly transverse. The pectorals are united with the head and trunk to form a subtriangular disk which is about a third of the total length and merges into the tail portion. Ventrals remote from the pectorals.

Only one species is known, confined to the warmer parts of the Indo-Pacific.

THE ROUND-SNOUT ANGELFISH

Rhina ancylostoma Bl. & Schn.

Rhina ancylostomus

Bloch & Schneider, *Syst. Ichth.*, page 352, plate 72, 1801; Coromandel; Indian Sea.

Gray, *Illustrations Indian Zoology,* vol. 2, plate 102, fig. 2, 1832-34; India.

Müller and Henle, *Plagiostomen,* p. 110, 1841.

Gray, *List Fishes Brit. Mus.,* p. 92, 1851; Madras; Pinang; China.

Bleeker, *Verh. Bat. Gen.,* vol. 24, 1852, *Plagiostomen,* p. 56; Batavia, Java.

Whitley, *Fishes Australia,* Part 1, Sharks, p. 179, figs. 205-206; 1940; Queensland and Broome, Western Australia.

Rhina ancylostoma

van Hasselt, *Algem. Konst. en Letterbode,* 1823; Java.

Jordan and Fowler, *Proc. U.S. Nat. Mus.,* vol. 26, p. 643, 1903; Kinkwazan, off Matsushima Bay, Japan.

Norman, *Proc. Zool. Soc. London,* p. 943, fig. 1 A, 1926; east Africa; Red Sea; Indian Ocean; Indian Archipelago; Australia; Japan.

Fowler, *Bull. 100 U.S. Nat. Mus.,* vol. 13, p. 299, 1941; after Day; the Philippines and 12 other localities.

Herre, *Check List Phil. Fishes,* p. 35, 1953; China Sea, southwest of entrance to Manila Bay.

Rhamphobatis ancylostomus

Dumeril, *Hist. Nat. Elasmobr.,* vol. 1, p. 482, 1865.

Annandale, *Mem. Indian Mus.,* vol. 2, p. 10, pl. 5, fig. 5, 1909; off Orissa; off mouth of river Hugli.

Garman, *Memoirs Mus. Comp. Zoology,* vol. 36, p. 267, 1913; Africa; China; East Indies.

Chevey, *Inst. Oceanogr. Indo-Chine,* 19e note, p. 7, 1932; Cochin China.

Rhynchobatus ancylostomus

Gunther, *Cat. Fishes Brit. Mus.,* vol. 8, p. 440, 1870; Madras; China; Seychelles; Pinang.

Day, *Fishes India,* p. 730, pl. 193, fig. 3, 1878; Madras.

Kent, *Great Barrier Reef,* p. 305; 1893; Queensland.

Tirant, *Service Oceanogr. Peches Indo-China,* 6e note, p. 72, 1929; Cochin China.

This is the easiest of our guitarfishes to recognize, for no other has its unique short broadly rounded or semicircular snout. Teeth in 77 rows above, 75 in the lower jaw. Spiracle as large as the eye, without folds. Nostrils half as long as width of mouth, and 1.5 times in the distance between the nostrils. The disk is almost a third of the total length, broader than its length. The fifth dorsal is large, triangular, the second dorsal perceptibly smaller; ventrals small; caudal rather large, lunate, the upper lobe larger; tail depressed, with a keel on each side.

A row of large spines or tubercles extends along each rostral ridge and above the inner margin of each eye to the nape; a row of still larger ones is along the middle of the back, but does not extend to the first dorsal; two more short parallel rows are over each shoulder; smaller tubercles are on the ridge before the eye.

The color is grayish or gray, the caudal paler, the entire upper surface except the head covered with white or nearly white spots which extend upon the dorsals, pectorals, ventrals, and caudal; curving lines and bars of black are more or less prominent on the head, pectorals, and disk. The under side is whitish. Some authors state that adults are uniform brown, but the color notes given are from a specimen two and a half meters long.

The round snout feeds largely on shrimp, crabs, and other crustacea, and is said by some to be a scavenger, but there is no direct evidence of this. The flesh is good and the dorsal fins are the very finest of all for that Chinese epicurean delight, sharkfin soup.

The only specimen positively identified by me from Philippine waters was the one referred to above. It was taken by otter trawl at a depth of 35 fathoms in the China Sea, off the south entrance to Manila Bay. For a good many years I have puzzled over the source of the white-spotted "shark" fins which are the choicest and most expensive of all the fins used for sharkfin soup. These fins, seen on the drying racks at Sitankai, Siasi, and all through the Sulu Islands and along the coast of Borneo, and in the shops of the Chinese dealers in Jolo and Zamboanga, could not be those of any known shark and I could never get hold of the fish from which they were taken. But now it is plainly evident that they are the fins of this ray, the Round-snout. It is therefore commonly taken by the Bajau and Samal fishermen from Sitankai to Palawan and Mindanao. It cannot be said to be abundant in Philippine waters but is certainly not a rare fish. Because its fins fetch the highest price it is a fish of some economic value. When normal trade relations are re-established, the trade in shark fins should be placed on a sound basis, with proper regulations enforced to secure fins of the highest quality. Without doubt it could be secured in larger quantities and its dried fins add considerably to the income of Sulu Province.

Nothing definite seems to be known about whether this fish furnishes sport to anglers or not. Outside the Philippines and East Indies the round-snout angelfish is known along the Asiatic coast from China and southern Japan to Indo-China and Malaya, southeast to Australia, westward to India, Ceylon, the Red Sea and the east coast of Africa.

GUITARFISHES

Genus RHINOBATOS Linck

Rhinobatos

LINCK, *Magazin Neustes Phys. Naturgas. Gotha,* ser. 3, vol. 6, p. 32, 1790; type *Raja rhinobatos* Linnaeus.
FOWLER, *Bull. 100, U.S. Nat. Mus.,* vol. 13, p. 304, 1941.

Rhinobatus

BLOCH & SCHNEIDER. *Syst. Ichth.,* p. 353, 1801.
MÜLLER and HENLE, *Plagiostomen,* p. 113, 1841.
GÜNTHER, *Catalog Fishes,* vol. 8, p. 441, 1870; in part.
DAY, *Fishes India,* p. 731, 1878.
GARMAN, *Memoirs Mus. Compar. Zool.,* vol. 36, p. 269, 1913; in part.
NORMAN, *Proc. Zoo. Soc. London,* No. LXII, p. 944, 1926.

Leiobatus

RAFINESQUE, *Carat. animal plante Sicilia,* p. 16, 1810; type *Leiobatus panduratus* Raf.

Squatinoraja

NARDO, *Osserv. Agg. Adriaticae Ittiol.,* 1824; type *Squatinoraja colonna* equals *Rhinobatus columnae* Müller and Henle.

Leiobatis

BLAINVILLE, *Faune Franc., Poiss.,* p. 43, 1825; type *Leiobatus panduratus* Raf.

Rhinobatis

BLAINVILLE, *Faune Franc., Poiss.,* p. 47, 1825.

Rhinobates

SWAINSON, *Nat. Hist.,* vol. 2, Fishes, p. 193, 1839.

Syrrhina

MÜLLER and HENLE, *Plagiostomen,* p. 113, 1841; in part.

Glaucostegus

BONAPARTE, *Cat. metodico pesci Europei,* p. 14, 1845; orthotype *Glaucostegus cemiculus* Bonaparte, equals *Rhinobatus cemiculus* Geoffroy St. Hilaire.

Key to the Species of Rhinobatos in the Philippines and Adjacent Seas

A.* (Rhinobatos) Forward nasal valve does not extend inward upon space between nostrils, or barely does so.

B. Length of nostril is twice or almost twice in width of mouth, and about equal to space between nostrils.

C. Snout long, narrow, its length 2.6 to 3.25 times width of mouth; rostral ridges parallel, very close together except near base .... R. GRANULATUS

CC. Snout broad, triangular, its length 1 and 5/6 times width of mouth; rostral ridges more or less separated for entire length; distance between spiracles 2.2 to 2.3 times in distance from eyes to snout tip .... R. OBTUSUS

BB. Length of nostril less than twice in width of mouth and more than distance between nostrils.

D. Snout distinctly enlarged at tip; nostril length 1.25 times in width of mouth, and about 1.75 times the space between nostrils .... R. THOUIN

DD. Snout not enlarged at tip.

E. Nostril length nearly equal to width of mouth and 2.3 to 2.5 times greater than distance between nostrils; preoral length of snout about 3 times width of mouth .... R. ARMATUS

EE. Nostril length 1.3 to 1.6 in width of snout and in distance between nostrils; preoral length of snout 2.6 to 2.66 times in width of mouth .... R. HALAVI

AA. (Leiobatus) Forward nasal valve extends inwards more or less upon the space between nostrils.

F. Anterior nasal valve extending inwards but little beyond inner edge of nostril and falling much short of reaching its opposite.

G. Rostral ridges more or less separated along whole length except at tip of snout; distance from outer extremity of nostril to lateral edge of snout slightly less than length of nostril .... R. FORMOSENSIS

GG. Rostral ridges very close together for anterior two-thirds of length; distance from outer rim of nostril to lateral edge of snout more than nostril length .... R. SCHLEGELI

ROUGH-BACKED GUITARFISH

Rhinobatos granulatus Cuvier

Rhinobatus granulatus
Cuvier, *Regne Animal,* ed. 2, vol. 2, p. 396, 1829.

Blyth, *Journ. Asiatic Soc. Bengal*, vol. 29, p. 36, 1860; Calcutta, India.
Günther, *Cat. Fishes*, vol. 8, p. 443, 1870; in part.
Martens, *Preuss. Exped. Ost-Asien*, vol. 1, p. 409, 1876; Bangkok, Siam, and Singapore.
Day, *Fishes India*, p. 732, pl. 192, fig. 2, 1878; Malabar; in part.
Volz, *Revue Suisse Zool.*, vol. 12, p. 484, 1904; Padang and Kwala, Sumatra.
Garman, *Mem. Mus. Comp. Zool.*, vol. 36, p. 272, 1913; India.
Norman, *Proc. Zool. Soc. London*, p. 949, text fig. 3, 1926; type of *Rhinobatos spinosus;* Madras; India; Shanghai; coasts of India, Ceylon, China.
Pillay, *Journ. Nat. Hist. Bombay*, vol. 33, p. 352, 1929; Travancore, India.
Chevey, *Inst. Oceanogr. Indo-Chine*, 19e note, p. 7, 1932; Indo-China.
Hora and **Mukerji**, *Records Indian Mus.*, vol. 38, pp. 18 and 21, pl. 2, fig. 1, 1936; Maungmagan, Burma.

Rhinobatus (*Rhinobatus*) *granulatus*
Müller and **Henle**, *Plagiostomen*, p. 117, pl. 38, 1841; Tranquebar and Pondicherry, India.
Bleeker, *Verh. Bat. Gen.*, vol. 25, 1853; Bengal, p. 82.
Duméril, *Hist. Nat. Elasmobr.*, vol. 1, p. 493, 1865. Malabar, Ganges River, and Pondicherry, India.

Rhinobatus tuberculatus (Cuv.)
Bleeker, *Verh. Bat. Gen.*, vol. 25, 1853; Bengal, p. 82.

Rhinobatus spinosus
Günther, *Cat. Fishes.*, vol. 8, p. 518, 1870; the type locality, "Mexico", is an error.

Rhinobatus thouini
Day, *Fishes India*, p. 732, pl. 190, fig. 4, 1878; Andaman Islands; not of Shaw.

Rhinobatis granulatus
Annandale, *Mem. Indian Museum*, vol. 2, p. 14, 1909; off Orissa, Bay of Bengal.

Rhinobatus acutus
Garman, *Mem. Mus. Comp. Zool.*, vol. 36, p. 273, pl. 17 b, figs. 1-2, 1913; Ceylon.

Rhinobatus granulatus

FOWLER, *Bull. 100, U.S. Nat. Mus.*, vol. 13, p. 316, 1941; Cebu; west coast of Palawan; Sandakan; Port Moresby, New Guinea.

The long pointed snout is slightly concave to straight along its margins, its length 1.3 to 1.4 in the head or the distance from eye to snout tip equal to distance from eye to posterior angle of pectoral; length from eye to tip of snout 3.3 to 3.6 times the distance between the spiracles; its length from the mouth is 2.6 to 3.2 times the width of the mouth. The narrow rostral ridges are very close together for more than half their length, diverging posteriorly. Diameter of eye about 9 times in the pre-orbital length of snout in the young, and 12 to more than 13 in adults. Spiracles behind and very near eyes and not much smaller, the folds little developed or the inner one absent. Nostrils oblique, twice or nearly twice in the slightly curved mouth. First dorsal about twice as high as the length of its base, its origin more or less twice as far behind the ventrals as the distance between the two dorsals, which are subequal in size.

Skin rough to the touch with a row of 15 to 30 large strong spines along the middle of the back from the head to the first dorsal; there may be one or more between the dorsals; rows of smaller spines occur on the shoulders, around the eyes and spiracles, and along both rostral ridges. With age the spines become blunt and less prominent.

The color is more or less reddish brown above, the snout often much paler with translucent margins, the dorsals usually gray; the under side is white or whitish.

This large guitarfish reaches a length of two and a third meters or more, though I have seen no Philippine specimens more than one and three-fourths meters in length. It occurs generally throughout the Philippines, especially among the islands and reefs of the Sulu and China Seas. It lives on flats which may have no more than a meter or two of water at low tide, down to at least 65 fathoms. One was taken by trawl at this last named depth in the China Sea south of Bataan Peninsula. It is seen in the Cebu market, on the drying mats of Sulu Province, and is taken at the mouth of Malampaya river and in Malampaya Sound; it is frequently caught on the flat sandy shores of the region about Sandakan, Borneo. It is to be expected in the Gulf of Lingayen.

Its range extends to the coast of China and throughout the East Indies to Australia, Indo-China, Malaya, India, Ceylon, the Red Sea, and the east coast of Africa.

THE TRIANGLE-SNOUT GUITARFISH

Rhinobatos obtusus Müller and Henle

Rhinobatus (*Rhinobatus*) *obtusus*

Müller and Henle, *Plagiost.*, p. 122, pl. 37, fig. 2, 1841; India; Pondicherry; Malabar.

Duméril, *Hist. Nat. Elasmobr.*, p. 493, 1865; Malabar; Indies; Pondicherry.

Rhinobatus obtusus

Günther, *Cat. Fishes*, vol. 8, p. 443, 1870; East Indies.

Norman, *Proc. Zool. Soc. London*, No. LXII, p. 950, text fig. 4, 1926; India; East Indies.

Rhinobatos obtusus

Fowler, *Bull. 100, U.S. Nat. Mus.*, vol. 13, p. 317, 1941; after Norman.

Rhinobatus halavi

Day, (not of Forskal), *Fishes Indit*, p. 731, pl. 193, (not 192 as given by Norman and Fowler), fig. 4, 1878; Mangalore.

The short broad bluntly pointed snout forms an equal sided triangle, the distance from the origin of the pectoral to the tip of the snout being equal to the distance across the base of the snout in a specimen over two meters long; margins of the snout slightly concave in same specimen; rostral ridges diverging anteriorly and posteriorly and well separated throughout. Eye about 7.3 times in the preorbital length of the snout; Norman gives 8 for specimens less than a meter in length. Only the outer fold of the spiracle is developed; spiracles about as large as eyes, and immediately behind them. Nostrils rather long, oblique, their length twice in that of the mouth and nearly equal to the distance between their inner ends. The narrow high and pointed first dorsal is about twice as high as its basal length. The origin of the first dorsal is twice or more than twice as far behind the base of the ventrals as the distance between the two dorsals; the second dorsal a little lower than the first. The rather large caudal is lunate with narrow lobes. There is a row of denticles or tubercles down the middle of the back, with smaller denticles on top of the head and on the shoulders. The spinal row is continued between the two dorsals. Some of those above the backbone may be spinous, but with age they become flattened and the body may be nearly smooth.

The color is gray to reddish gray or brownish gray above, the dorsals and caudal paler, the under side whitish to white. The head, disk, and trunk back to the second dorsal are sprinkled with small white or whitish spots, which may be arranged in 4 or 5 longitudinal rows along each side of the body, and may also be in rows on the pectorals.

A specimen over two meters long was taken by otter trawl off the east coast of Panay, near Guimaras Island. This is the only positive Philippine record to date, but no doubt it is of general occurrence from Luzon southward. It is known from the East Indies and the shores of India and southward in the Indian Ocean to Natal.

Rhinobatos thouin (Anonymous)

Raja thouin

Anonymous, *Allgem. Lit.-Zeit.*, vol. 3, pp. 287, 677, 685, pl. 1, figs. 3 and 4, 1798.

Raia thouiniana

Shaw, *General Zool.*, vol. 2, p. 318, pl. 147, fig. 2, 1804. On *La raie thouin Lacépède, Hist. Nat. Poiss.*, vol. 1, p. 134, pl. 1, figs. 3-5, 1798.

Rhinobatus thouini

van Hasselt, *Algem. Konst. Letterbode*, 1823, Java. *Bull. Sci. Nat. Ferussac*, vol. 2, p. 90, 1824; Java.

Günther, *Cat. Fishes*, vol. 8, p. 442, 1870; Penang; East Indies.

Weber, *Siboga Exped.*, Fische, vol. 57, p. 597, 1913; Makassar and Aru Islands.

Garman, *Mem. Mus. Comp. Zool.*, vol. 36, p. 276, 1913; Penang.

Chabanaud, *Bull. Econom. Indo-Chine*, vol. 6, No. 169, p. 563, 1924; Gulf of Siam.

Suvatti, *Index Fishes Siam*, p. 4, 1937; Canthaburi; Samut Prakan; Maenam Wen, East Coast.

Rhinobatus (*Rhinobatus*) *thouini*

Müller and Henle, *Plagiostomen*, p. 120, 1841.

Dumeril, *Hist. Nat. Elasmobr.*, vol. 1, p. 500, pl. 10, fig. 2, a-b, 1865; Red Sea.

Rhinobatus thouinianus

Fowler, *Proc. Acad. Nat. Sci. Philadelphia*, p. 460, 1904; Baram, Borneo.

Rhinobatus thouiniana

Norman, *Proc. Zool. Soc. London*, 1926, p. 951, 1926; Penang; Malay Archipelago.

Rhinobatus thouin

Fowler, *Bull. 100, U.S. Nat. Mus.*, vol. 13, p. 317, 1941; after Norman.

Rhinobatus (*Rhinobatus*) *ligonifer*

Cantor, *Journ. Asiatic Soc. Bengal*, vol. 18, p. 1397, pl. 14, 1849; Penang; Malay Peninsula; Singapore.

Bleeker, *Verh. Bat. Gen.*, vol. 24, 1852; *Plagiostomen*, p. 59; Bantam and Samarang.

The rather long snout has its tip distinctly enlarged so that its margins are definitely concave, its length from eye to tip 3.3 to 3.6 times the distance between the spiracles; its length from mouth to tip is 3 times the width of the mouth. Rostral cartilage narrow, wider anteriorly, the ridges close together most of their length. The eye is 7 to 8.75 times in the snout, measured from tip to eye. Both folds of the spiracle are poorly developed, the outer one more prominent. The oblique nostrils are nearly twice as long as the space between them, and are about 1.3 times in the width of the mouth; the anterior valve does not extend inwards. First dorsal about twice as high as the length of its base; its origin is 1.2 to 1.25 times as far behind the base of the ventrals as the distance between the dorsals; second dorsal nearly equal to the first; caudal long, narrow, and pointed.

There are enlarged denticles or tubercles above the spine and smaller ones in front of each eye, above the spiracles; two on each shoulder, the inner one the larger.

The color is light rusty brown, the dorsals and caudal fin darker; the under surface varies from little paler to yellowish white.

The peculiar widened tip of the snout separates this guitarfish at once from all others. I have no specimens from the Philippines, but have observed it on the drying racks at Sitankai. It is common all along the northern coast of Borneo and therefore occurs in Philippine waters from Sulu Province to Balabac. It is common in the fish market at Kuching, Sarawak, where I purchased several. It is said to reach a length of more than 1.75 meters, but I have seen none more than a meter long. It is rather abundant on the coast of Malaya, and ranges from Penang and Siam through the East Indies to New Guinea.

THE ARMED GUITARFISH

Rhinobatos armatus Gray

Rhinobatus typus

Bennett, *Life of Raffles*, p. 694, 1830; Sumatra.

Rhinobatus armatus

GRAY, *Illustrations Indian Zool.*, vol. 2, pl. 99, 1834.

PETERS, *Monatsber. Wiss. Akad. Berlin*, p. 853, 1877; Bougainville Island, Solomon Islands.

OGILBY, *Mem. Queensland Mus.*, vol. 5, p. 85, fig. 1, 1916.

NORMAN, *Proc. Zool. Soc. London*, p. 952, text fig. 6, 1926; India; Singapore; Makassar; Sumatra; Cape York, North Australia; Groote Eylandt, Northwest Territory; Western Australia.

HERRE, *Journ. Pan Pacific Research Inst.*, vol. 8, 1933; p. 2, Sandakan, Brit. North Borneo.

HERRE, *Fishes 1931 Phil. Exped.*, p. 12, 1934; Sitankai, Sulu Province.

Rhinobatus (Rhinobatus) armatus

MÜLLER and HENLE, *Plagiostomen*, p. 119, 1841; India.

BLEEKER, *Verh. Bat. Gen.*, vol. 23, p. 13, 1850; Java.

BLEEKER, *Nat. Tijds. Ned.-Ind.*, vol. 3, p. 85, 1852; Singapore.

BLEEKER, *Acta Soc. Sci. Indo-Neerl.*, vol. 1, p. 10, 1856; Makassar, Celebes.

BLEEKER, *Ibid.*, vol. 6, p. 3, 1859; Doreh, New Guinea.

DUMÉRIL, *Hist. Nat. Elasmobr.*, vol. 1, p. 494, pl. 10, fig. 4 (scutes), 1865.

Rhinobatus granulatus

GÜNTHER, *Cat. Fishes*, vol. 8, p. 443, 1870; in part; not of Cuvier.

DAY, *Fishes India*, p. 732, 1878.

Rhinobatus halavi

GARMAN, *Mem. Mus. Comp. Zool.*, vol. 36, p. 275, 1913; in part, exclud. synonymy; Southern Celebes and Singapore.

Rhinobatos armatus

HERRE, 1936–37 Exped.; Sandakan, North Borneo.

Rhinobatos typus

FOWLER, *Bull. 100, U.S. Nat. Mus.*, vol. 13, p. 319, 1941; after NORMAN.

This large guitarfish reaches a length of more than two meters, though Norman's largest specimen was but 550 mm. long. Specimens up to a meter and a half long are taken in the Sibutu Islands.

The head is pointed, the snout bluntly rounded, its margin slightly concave. From the eye to the tip of the snout is 3 to 3.2 times the distance between the spiracles, and from the mouth to the snout tip is 2.5 times the width of the mouth. The rostral ridges are close together, only diverging a little posteriorly. The eye is 6.2 to 8.2 in the preorbital length of the snout, with age the eye becoming proportionately smaller. The large spiracles are close behind the eyes, each with two feeble folds on its rear margin, the outer one more prominent. The large oblique nostrils are five-sixths of or nearly equal to the width of the mouth, and 2.5 to 3 times as long as the space between their lower or inner ends. The first dorsal is twice or more than twice as high as the length of its base; the distance of its origin behind the base of the ventrals is 1.3 to 1.6 times the distance between the two dorsals.

There is a row of rather strong compressed spines along the middle of the back, and one or two groups over each shoulder; there are usually several smaller spines around each eye and spiracle. The denticles on top of the head, on the back, and on the shoulders are larger than elsewhere.

The color above is gray, shading to yellowish or reddish, but often the upper side is uniformly grayish brown; the lower surface is white, with a brown spot near the tip of the snout.

The armed guitarfish is common on the extensive reef sand flats about Sitankai and the other Sibutu Islands, Sandakan, and all along the north coast of Borneo. It is often seen on the drying platforms at Sitankai. No doubt it occurs also on the shores of Mindanao, Palawan, and the Visayan Islands. It ranges from the shores of India and Malaya through the East Indies to the Solomon Islands and tropical Australia.

Rhinobatos halavi (Forskal)

Raja halavi
FORSKAL, *Descrip. Anim.*, p. 19, 1775.

Rhinobatus halavi
RÜPPELL, *Atlas, Fische,* p. 55, pl. 14, fig. 2, 1828.
GÜNTHER, *Cat. Fishes,* vol. 8, p. 442, 1870; in part.
KLUNZINGER, *Verh. zool.-bot. Gesells. Wien,* vol. 21, (Synopsis Fische Roth. Meeres, part II, p. 235) 1871.
NORMAN, *Proc. Zool. Soc. London,* p. 956, text fig. 9, 1926.

Rhinobatus (*Rhinobatus*) *halavi*
MÜLLER and HENLE, *Plagiostomen,* p. 120, 1841.
DUMÉRIL, *Hist. Nat. Elasmobr.*, vol. 1, p. 496, 1865.

Rhinobatos halavi
FOWLER, *Bull. 100, U.S. Nat. Mus.*, vol. 13, p. 320, 1941.

Rhinobatus granulatus
BAMBER, *Journ. Linn. Society London, Zool.*, vol. 31, p. 477, 1915; not of CUVIER.

The nearly triangular snout is of moderate length, with bluntly rounded tip, the nearly straight margins slightly concave; the preorbital length is about 1.35 times in its width and 2.75 to 3 times the distance between the spiracles; the length from mouth to tip of snout is 2.6 to 2.66 times the width of the mouth. The narrow rostral ridges are close together most of their length, diverging a little anteriorly and posteriorly. The eye is contained 5 to 6 times in the preorbital length of the snout; spiracles deep but much smaller than the eyes, and close to them, with two folds on each rear margin, the inner one small. Nostrils oblique, medium in size, their length about 1.5 times in the width of the mouth. The first dorsal is twice as high as its basal length; the distance of its origin from the base of the ventrals is 1.66 to nearly twice in the space between the two dorsals.

The skin is smoother than in most guitarfishes but the denticles on top of the head, shoulders, and back are enlarged; a row of 15 to 20 spines from the head to the first dorsal and a single (2?) spine between the dorsal fins. Usually there are 2 or 3 large spines on the ridge before the eye and above each spiracle, and one or two spines on each shoulder. Young specimens have a row of spines along each ridge of the snout. With age all spines tend to become smooth or to disappear.

The color is olive brown above, becoming more or less reddish brown along the margins of the head and disk; under surface white or whitish.

The recorded length is 1500 mm., and it probably reaches 2 meters.

No specimens have been seen from Philippine waters, but it was recorded in 1895 by Casto de Elera from the Gulf of Lingayen, La Union Province. It may very well occur there and indeed all along the western coast of the Philippines, from Balabac to Ilocos Norte. It should be looked for carefully on the west coast of Palawan, especially in the fish corrals of Malampaya Sound, and in the trawler catches of the Gulf of Lingayen.

Its known range is from the Red Sea all along the coast of Asia to China. It has also been reported from Australia.

THE FORMOSA GUITARFISH
Rhinobatus formosensis Norman

Rhinobatos formosensis

NORMAN, *Proc. Zool. Soc. London,* No. LXII, p. 958, text fig. 11, 1926; type locality, Formosa.

FOWLER, *Bull. 100, U.S. Nat. Mus.,* vol. 13, p. 307, 1941; after NORMAN.

HERRE, *Check List Phil. Fishes,* p. 37, 1953.

The long bluntly pointed snout is rather narrow, its preorbital length almost equal to its width at the upper margin of the eyes; the preoral length is 3.5 to 3.66 times the width of the mouth. The eye is 4.3 to 4.6 times in the preorbital length of the snout. The spiracles are much smaller than the eyes and immediately behind them; the outer fold of the spiracle is well-developed, the inner one small. The narrow rostral ridges are separated more or less almost their whole length, converging and very close together at their tip, diverging posteriorly. The oblique nostrils are of moderate size, their length 1.4 to 1.5 times in the width of the mouth, and about 1.5 times as long as the space between their inner ends.

The height of the first dorsal is less than twice its basal length; its origin is behind the ventral base a distance equal to or greater than the space between the two dorsals.

The skin is smooth to the touch, its denticles minute. There is a row of rudimentary tubercles along the midline of the back, around the eyes, and the spiracles, so small as to be scarcely visible to the naked eye.

This guitarfish was described by Norman from two specimens from Formosa, 625 and 630 mm. in length. A larger specimen, almost a meter in length, was determined by the well-known Filipino ichthyologist, A. F. Umali. It was taken by otter trawl in the China Sea off the south entrance to Manila Bay, at a depth of 65 fathoms, or over 118 meters. No doubt it occurs in the deeper parts of Manila Bay, near Corregidor, and all along the western coast of Luzon, particularly in the Gulf of Lingayen.

Rhinobatos schlegeli Müller and Henle

Rhinobatus schlegeli

MÜLLER and HENLE, *Plagiostomen*, p. 123, pl. 42, 1841; Nagasaki.

Rhinobatus schlegelii

RICHARDSON, *Ichthy. China Japan*, p. 195, 1846.

GÜNTHER, *Cat. Fishes*, vol. 8, p. 445, 1870; Japan but not Formosan specimen.

ELERA, *Cat. Fauna Filip.*, vol. 1, p. 619, 1895; Navotas, Manila, Luzon; a dubious reference.

STEINDACHNER, *Ann. Hofmuseum Wien*, vol. 11, p. 225, 1896; Kobe, Hiogo, Nagasaki.

GARMAN, *Mem. Mus. Comp. Zool.*, vol. 36, p. 276, 1913; Japan.

NORMAN, *Proc. Zool. Soc. London*, No. LXII, p. 959, fig. 12, 1926; Japan.

Rhinobatus schlegeli

Schlegel, *Fauna Japonica, Poiss.*, p. 307, 1848 (1950) Nagasaki Bay.

Jordan and Snyder, *Proc. U.S. Nat. Mus.*, vol. 23, p. 337, 1900; Tokyo.

Jordan and Evermann, *Proc. U.S. Nat. Mus.*, vol. 25, p. 318, 1902; Formosa.

Tanaka, *Jap. Fish. Life Colors*, No. 29, 1933.

Rhinobatus schlegel

Jordan and Fowler, *Proc. U.S. Nat. Mus.*, vol. 26, p. 646, 1903; Tokyo, Wakanoura, Onomichi, Hakata, Nagasaki.

Rhinobatos schlegeli

Mori, *Journ. Pan Pacif. Research Inst.*, vol. 3, p. 3, 1928; Fusan and Mokpo, Korea.

Fang and Wang, *Contrib. Biolog. Lab. Sci. Soc. China,* vol. 8, p. 259, fig. 19, 1932; Tsingtau, China.

Rhinobatus schlegelii

Fowler, *Bull. 100, U.S. Nat. Mus.*, vol. 13, p. 308, 1941; Simoda, Wakanoura, Hakata, Japan.

The snout is long, with bluntly rounded tip and concave margins; the rather narrow parallel rostral ridges are very close together anteriorly, diverging a little posteriorly. The eye is 4.85 to nearly 5 times in the preorbital length of the snout; the small spiracles are very close to the eyes, their folds little developed, the outer one more evident than the inner. The short nostrils are rather broad, 1.6 times in the width of the mouth, and 1.3 to 1.4 times more than the space between their inner ends. The height of the pointed first dorsal is about twice the length of its base. The origin of the first dorsal is a little farther from the ventral base than the distance between the two dorsals.

The skin is smooth to the touch, though covered with minute denticles. A row of about 3 dozen small blunt tubercles or spines extends down the middle of the back; small spines are present or absent around the eyes and above the spiracles; none are on the shoulders.

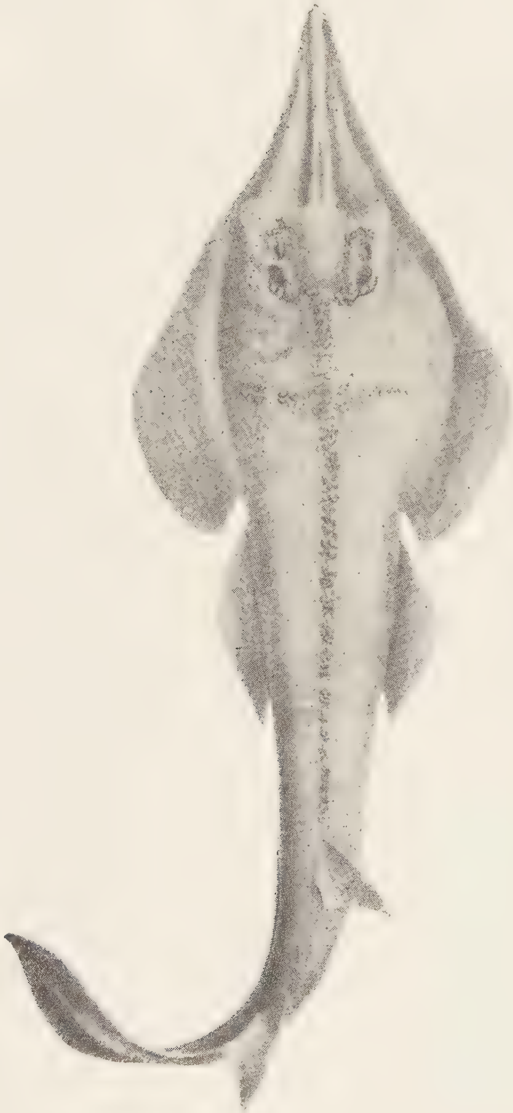
The color is brown above, mottled or speckled with darker, the sides of the snout translucent or paler brown. The under surface is whitish, except for a black or dusky blotch under the tip of the snout. The young may have many widely scattered small rounded whitish spots over the disk and trunk.

For a long time this guitarfish, which reaches a length of about a meter, was only known from Japan, but it also occurs on the shores of Korea, China and Formosa. It was reported from Manila Bay by Casto de Elera but his determinations are often too doubtful to be accepted without later confirmation. However in view of its distribution it may well be in Philippine waters. It should be looked for in the Gulf of Lingayen and the north coast of Cagayan Province, Luzon, as those waters contain many Formosan fishes.

The white-spotted guitarfish, known as Pating sodsod—*Rhynchobatus djiddensis* (Forskal).

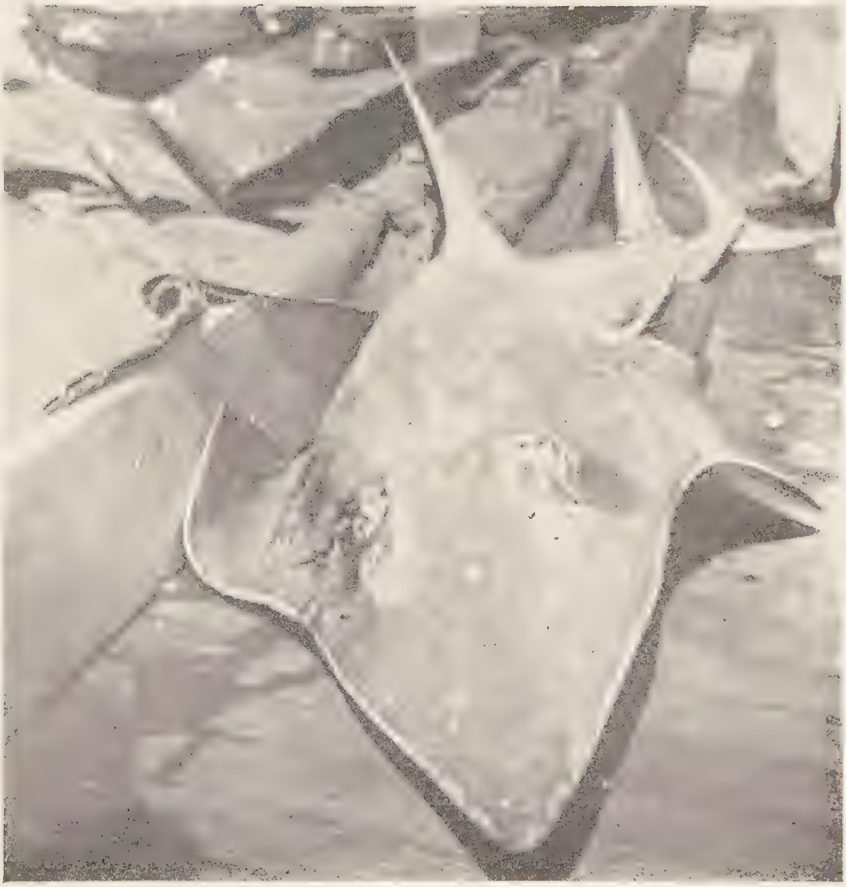
A fine specimen of Pating sodsod over 2 meters long, from the China Sea off Cavite Province.

A Round-snout Guitarfish (*Rhina ancylostoma* Bl. & Schn.). Over two rs long. Caught near entrance to Manila Bay.

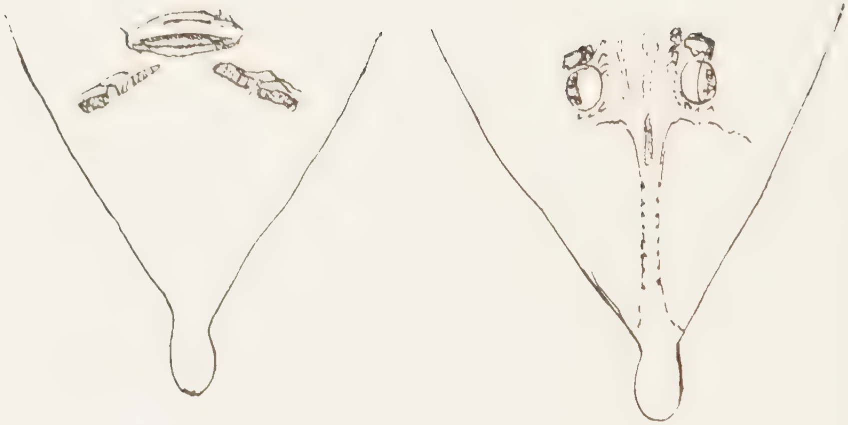


Rough-backed Guitarfish *Rhinobatus granulatus* Cuvier.

[illegible] meters long, from the [illegible]



A specimen of *Rhinobatus obtusus* from the east coast of Panay. It was over 2 meters long.



Characteristic outline of snout of *Rhinobatus thouin*. Left—upper surface; right—lower surface. (After Norman)

POPULATION STUDIES AND SOME ASPECTS OF THE ECOLOGY OF POTATO APHIDS IN SELECTED AREAS IN CANTERBURY, NEW ZEALAND

By B. B. Watts

Synopsis

In this paper, "Population Studies and Some Aspects of the Ecology of Potato Aphids in Selected Areas in Canterbury, New Zealand," some short reference is made to previous writings on the subject. Investigational work on a potato aphid survey at Lincoln and Darfield is described. Some aspects of the ecology of the three species concerned have been presented. Some laboratory studies and overwintering work have also been carried out. Finally some tables are presented giving aphid numbers and virus records.

The three species of aphids found on potato crops in New Zealand have been identified as *Myzus persicae* Sulz, *Aulacorthum solani* Kitb (*Myzus pseudosolani* Theobald) and *Macrosiphum euphorbiae* Thomas (*solanifolii* Ashm, *gei*-Koch). The life cycle and overwintering habits of these three species have been investigated. Fewer aphids were found in the Darfield district than in the Lincoln district and a relationship has been found between climatic conditions, particularly relative humidity and aphid numbers. The possibility of forecasting when to spray the crops for aphids has been considered. After a more extensive study of weather conditions and how they affect aphid numbers, such a forecasting plan may be possible.

Introduction

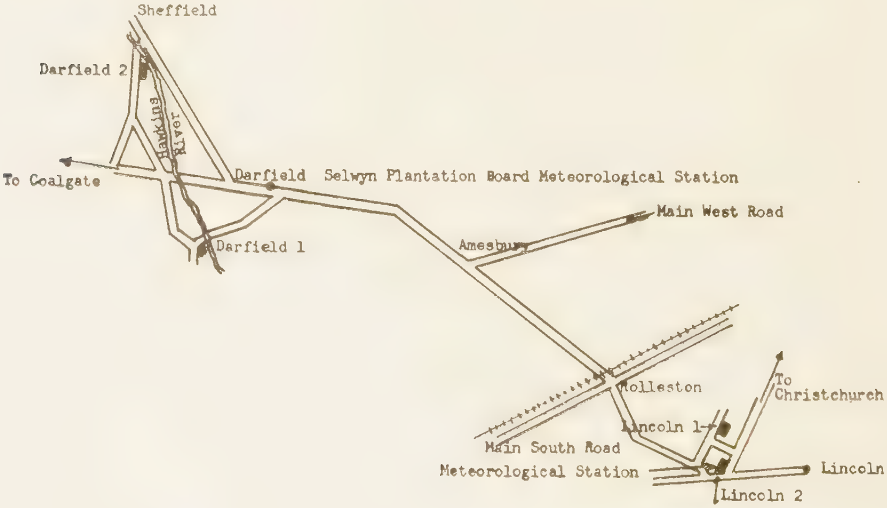
One of the most important diseases of potatoes which is degeneration or "running out" was first observed in 1770. Today we know that degeneration is caused by viruses, the most important being leaf roll, virus Y (rugose mosaic) and virus X (slight mosaic). Virus Y was found to be aphid transmitted by Schultz, *et al.* (1919) and two years later leaf roll was found to be similarly spread by aphid vectors Schultz and Folsom (1921). The potato certification scheme, which in New Zealand was put into operation in 1931, is concerned with the maintenance and distribution of seed true to type and relatively free from virus. In New Zealand it has been found that in certain areas, certified seed can be grown more successfully than in other areas, but apart from one extensive survey done by Cottier (1931) no work has been done on aphid populations on potato crops in this country.

Most of the early work on potato aphid populations was done in England by Davis (1932), who worked out an ‘index” figure of aphid infestation, being the figure which would give some indication of the numbers and movement of the alate, which are the greatest potential danger to a crop in a seed producing area. In further work Davies (1935) found that in those districts in which relative humidity was consistently low, aphid numbers were higher than in those districts where the relative humidity was consistently high. In a later publication Davies (1936) discusses the effect of wind on aphid flight, and points out the difference between active flight during which the aphid has full control over speed and direction and passive flight when the aphid is carried by the wind.

Broadbent and Gregory (1948) have shown that nearly half the total transmission of rugose mosaic and leaf roll had taken place soon after the period of tuber set, which would indicate that the alate spring migrants are responsible for most of the early spread of virus. This finding was also substantiated in work by Broadbent and Tinsley (1951) who found that 83% of rugose mosaic and 97% of leaf roll was transmitted by the alate *Myzus persicae*.

Investigational Work

1. *Locality of Survey:*—Four potato crops were sampled during the 1951-2 and 1952-3 seasons, as near as possible to weekly intervals. Two crops were in the Lincoln district—Lincoln 1 and Lincoln 2, and the other two crops were in the Darfield area—Darfield 1 and Darfield 2.


Sheffield
Darfield 2
Hawkins River
To Coalgate
Darfield
Selwyn Plantation Board Meteorological Station
Main West Road
Darfield 1
Amesbury
Rolleston
To Christchurch
Lincoln 1
Main South Road
Meteorological Station
Lincoln
Lincoln 2

The area of the crop, variety and date of sowing and aspect are given in Table I.

2. *Sampling and Identification:*—Thirty leaves were taken from each crop at each sampling, these being taken at every tenth step as the crop was traversed. In 1951–2 the samples were stored in K.A.A. solution (Kerosene—1 pint, 95% ethyl alcohol—1 part, acetic acid—2 parts), for identification during the winter. In 1952–3 the species were identified on the leaf with the aid of a binocular microscope.

The outstanding characteristics of the species concerned are those listed below.

Myzus persicae: Antennal tubercles strongly converging, cornicles slightly swollen (Fig. 1).

Aulacorthum solani: Antennal tubercles parallel, cornicles slender and not swollen (Fig. 2).

Macrosiphum euphorbiae: Antennal tubercles diverging, cornicles long and slender. (Fig. 3).

The aphids were divided into species and stage of maturity, the final number being expressed as aphids per thirty leaves.

Adhesive traps similar to those described by Broadbent *et al.* (1948) were set up at Lincoln 2 and Darfield 2. These traps consisted of a foot length of stove pipe five inches in diameter. The pipes were painted white and nailed to stakes, the lower edge of the trap being two feet above the ground. The traps were covered with plastic which was removed at each sampling, and a new cover was replaced. The cover was taken to the laboratory, the aphids picked off were washed into a tube containing 50–50 ethyl acetate and acetic acid. The tube was heated in a water bath held at 170–190 degrees Fahrenheit for 10–15 minutes to dissolve the grease, then the fluid was drawn off, phenol was added and the tube was returned to the water bath for a few minutes to clear the specimens.

3. *Overwintering Studies:*—Attempts were made to raise a culture of aphids indoors on potted savoy cabbages. Four peach trees were also grown in pots and placed near the savoys to ascertain whether the autumn migrants laid their overwintering eggs on the peach trees. Numerous plants and weeds were inspected for overwintering aphids and a survey was made of the peach trees around the Cashmere Hills near Christchurch in 1952.

RESULTS OF SURVEY

The results of the two seasons' sampling are presented in Table II and represented graphically in Figure 4. The readings of weather conditions were obtained from the Meteorological Stations at Lincoln College and Darfield and are superimposed on Figure 4.

A striking difference between the two seasons is the large numbers of *Aulacorthum solani* found on the crops at Darfield 1 and Darfield 2 in 1951–2. The numbers of *Aulacorthum solani* in 1952–3 at Lincoln 2 were high but did not at anytime reach the peak they reached at Darfield. *Myzus persicae* was more numerous on all crops in 1952–3 than in the previous season. The numbers of *Macrosiphum euphorbiae* were found to be very few, and showed a tendency to increase and reach their peak after *Myzus persicae* had reached their maximum.

1. *Meteorological Conditions:*—Weekly records for Lincoln and Darfield districts have been compiled and are shown in Table III. It should be noted that these readings are taken at 9 a.m. and do not show changes which may have taken place during the day.

The two seasons under consideration have been remarkable for the high rainfall and the high number of rainy days. There have been few of the usually prevailing north west winds in the six months under survey. A comparison of the two seasons is shown in Table IV.

2. *Trap Data:*—The results of the trapping are shown in Table V. The traps at Darfield were not set up until 28th December 1952 because of the late sowing of that crop. Consequently the trapping records for the 1952-3 season are not complete and cannot be correlated with weather records. There is a relationship between the number of aphids caught in the traps and the aphids caught on the leaves. More *Aulacorthum solani* were caught on the traps than *Myzus persicae* in both seasons but especially so in 1951-2.

3. *Virus Data:*—These figures are given to support the theory that potatoes grown at Lincoln have a higher incidence of virus than those grown in the Darfield-Springfield area. Lines of seed have been traced through from those growers who sell certified seed potatoes to growers in the Lincoln district. From Table VI it may be seen that the incidence of leaf roll in Aucklander Short Top increases from a small percentage when the seed is moved from Hororata to Prebbleton. Dakotas "run out" quickly when moved from Annat to Southbridge. The table shows an increase in aphid borne virus diseases when the seed is moved from Darfield-Sheffield district to the Lincoln district.

4. *Overwintering:*—*Myzus persicae*—Savoy cabbages were found to be supporting large populations of this aphid, especially on the lower leaves for as Ludwig (1945) points out, a moist environment is beneficial during exposure to low temperatures because the latent heat of water prevents a very rapid drop in temperature. *Myzus persicae* was found to be reproducing throughout the year and was taken from the

following plants during the winter: raddish, Shepherd's purse, fathen, mallow, cauliflower, young spring cabbage, beetroot, tomatoes, black nightshade, turnips, rape and chitting tubers.

Several surveys were made in peach growing districts and on no occasion were the eggs of *Myzus persicae* found. The savoy cabbages in the insectary supported a population of *Myzus persicae* throughout the winter, and potatoes planted in the insectary were colonized directly from the brassicas. *Aulacorthum solani* was not taken from cabbages at the College during the winter. This species was recorded on polyanthus in a sheltered garden at Lincoln College suggesting that it may have overwintered on this host.

Macrosiphum euphorbiae was found on sow-thistle early in the season, but further inspection from July onwards found no hibernating forms at the College in 1952. This species was not found on brassicas.

DISCUSSION

Overseas, *Myzus persicae* is regarded as being the most important vector of virus diseases and it is likely to be the most important virus vector in this country also. This aphid was recorded colonizing potatoes directly from brassicas. The spring migration of alate in the field appeared to commence in mid-November 1951. In early November 1952 the crop at Lincoln, although only three inches high, was infested at the rate of 3/30 leaves. From November onwards alate are quite plentiful and will readily infest potato crops.

The variation in aphid numbers which is seen to occur between the two seasons requires some explanation. The main overall factor which operated in 1952–3 was undoubtedly relative humidity, since this is the only factor which showed a wide change from one season to the other. The period of high relative humidity at Darfield 1 between 23 November and 5 December 1952 would lead to a reduction in the aphid population by depressing multiplication and by inhibiting flight.

The autumn migration from Darfield 1 began about the first week in January, and from Lincoln 2 in mid-January. At Lincoln in the years under survey the peach tree apparently did not provide a winter host for the eggs of *Myzus persicae*.

The lower numbers of *Myzus persicae* recorded in 1951 as compared with 1952 can be explained in part by the later commencement of sampling in the former year. The weather records in Table VII show that up to May 1951, the rainfall was high so that the overwintering population would probably have been lower than in 1952. In 1952 the initial overwintering population was high and *Myzus persicae* was found to be reproducing steadily throughout the year, and alate were found on savoy cabbages at all times during the winter.

The populations of *Aulacorthum solani* were higher in 1951–2 than those of either *Myzus persicae* or *Macrosiphum euphorbiae.* More *Aulacorthum solani* were taken at Darfield than at Lincoln in 1951–2, but in 1952–3 the reverse occurred. Since *Aulacorthum solani* was found hibernating only on polyanthus and dock, it is possible that the main overwintering form is the egg, which would be less affected by weather conditions. It also seems likely that the activity, flight and reproduction of *Aulacorthum solani* is affected more severely by high humidities than is *Myzus persicae.* The spring migrants had reached the potato crop by the first week in November and the autumn migrants left the potato crop in early January.

Macrosiphum euphorbiae was found only sparingly during 1951–2, and rainfall figures show there was less rain during the period in which the apterae were found. In both seasons rainfall was high in the spring and this can account in part for the low population of *Macrosiphum euphorbiae.* This species was the last to arrive on the crop in both seasons.

1. *The Importance of Aphids as Virus Vectors:*—In this country the activity of aphids on potatoes is of importance only in so far as they spread the virus diseases which lead to the running out of potatoes. *Myzus persicae* is recognized as the most important of the aphid vectors of virus diseases, being responsible for the transmission of over twenty different viruses. Doncaster and Gregory (1948) came to the conclusion that neither *Macrosiphum euphorbiae* nor *Aulacorthum solani* play any appreciable part in transmitting either leaf roll or rugose mosaic in the field. Table VIII, which is a summary of Table II shows that *Myzus persicae* is the most important vector of potato virus.

On the crop at Darfield 1, 142 *Aulacorthum solani* were taken in 1951–2 compared with 12 *Myzus persicae.* The seed from this crop was certified in 1953 as Mother 1, the highest grade. The same applies for Darfield 2 which was certified as Mother 2, the same grade as the previous year. The table also shows that whereas 355 *Myzus persicae* were taken from the two crops at Lincoln, only 107 were taken from the two Darfield crops. Since *Myzus persicae* is responsible for the transmission of most of the virus diseases, then it is to be expected that potatoes at Lincoln will "run out" more quickly than at Darfield, and that the latter area will be the more suitable for the growing of seed free from virus.

2. *Weather Conditions and Aphid Numbers in the Seasons under Survey:*—The effects of weather conditions on the activity of aphids are

important, and it is the influence of these weather factors which can explain some of the differences in aphid numbers found in this survey.

Wind has been considered to be especially important in overseas work as a factor influencing aphid numbers—Staniland (1943). No relationship was found between wind and aphid numbers in the two seasons under survey. The six months of the survey have been exceptional for the low incidence of the north-west winds which are the prevailing winds in the Darfield area.

Maximum temperatures have been slightly higher at Darfield than at Lincoln but this factor alone did not show any marked relationship with aphid numbers. However, the two factors, maximum temperature and relative humidity, act together in their influence on aphid flight and activity.

In a so-called normal season, in which north-west and north winds are the prevailing winds from November until March, it is quite possible that aphids could be blown down country. There is often a period of calm with usually fairly high temperatures and a low relative humidity, before the wind suddenly springs up. The aphid is thus at the mercy of the wind and may be blown by the wind dropping from the air stream in currents and downdraughts of air set up over trees and buildings.

For a more complete study of the problem, a five-year survey should be carried out. Weather conditions are of such prime importance that they cannot give a general picture applicable to all seasons. A thorough understanding of the effects of weather which could only be gained over a longer survey is, however, likely to help in making an early estimation of the incidence of virus.

ACKNOWLEDGMENTS

The writer wishes to thank Mr. L. Morrison, Senior Lecturer in Entomology at Lincoln College, Dr. Cottier of Cawthron Institute, Mr K. M. Doull and Mr. R. C. Blackmore of Lincoln College for their help and interest in this survey. Appreciation is also expressed to the four farmers whose crops the author sampled, without whose co-operation the study would not have been possible.

LIST OF REFERENCES

BROADBENT, L. and P. H. GREGORY. (1948). Experiments on the spread of rugose mosaic and leaf roll in potato crops in 1946. *Ann. Appl. Biol.* 35: 395-405.

BROADBENT, L., J. P. DONCASTER, R. HULL, and M. WATSON. (1948). Equipment used for trapping and identifying alate aphids. *Proc. Roy. Ent. Soc. Lond.* A.3: 57-8.

TABLE II

TOTAL APHIDS ON LEAVES

	LINCOLN 1				LINCOLN 2				DARFIELD 1				DARFIELD 2				
	M. persicae	*A. solani*	*M. euphorbiae*	TOTAL	*M. persicae*	*A. solani*	*M. euphorbiae*	TOTAL	*M. persicae*	*A. solani*	*M. euphorbiae*	TOTAL	*M. persicae*	*A. solani*	*M. euphorbiae*	TOTAL	TOTAL—ALL SPECIES
1951/2																	
Dec. 10	4	9	1	14	12	57	2	71	2	87	—	89	No Sample				174
Dec. 16	—	2	—	2	3	30	2	35	7	33	—	40	—	52	—	52	129
Dec. 23	—	—	—	—	1	7	3	11	2	10	—	12	5	28	—	33	56
Dec. 30	—	1	—	1	2	8	—	10	1	12	—	13	1	22	2	25	49
Jan. 6	—	—	—	—	—	1	—	1	—	—	—	—	—	7	—	7	8
Jan. 17	—	4	—	4	—	—	—	—	—	—	1	1	—	3	—	3	8
Jan. 20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Jan. 27	2	—	—	2	—	—	—	—	—	—	—	—	—	1	—	1	3
Feb. 3	—	3	—	3	—	—	—	—	—	—	—	—	—	—	—	—	3
Feb. 10	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	1
Feb. 17	3	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	3
Feb. 27	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mar. 1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	1
Mar. 12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Apr. 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total 1951/2	9	19	2	30	18	103	7	128	12	142	2	156	6	113	2	121	435

TABLE II (Continued)

	LINCOLN 1				DARFIELD 1				LINCOLN 2				DARFIELD 2				
	M. persicae	*A. solani*	*M. euphorbiae*	TOTAL	*M. persicae*	*A. solani*	*M. euphorbiae*	TOTAL	*M. persicae*	*A. solani*	*M. euphorbiae*	TOTAL	*M. persicae*	*A. solani*	*M. euphorbiae*	TOTAL	TOTAL—ALL SPECIES
1952/3																	
Nov. 15	3	1	—	4		No	Sample		6	—	—	6		No	Sample		10
Nov. 23	12	—	—	12		”	”		1	—	—	1		”	”		13
Nov. 30	21	9	—	30	18	7	—	25	—	—	—	—		”	”		55
Dec. 5	28	11	—	39	21	13	—	34	—	—	—	—		”	”		73
Dec. 12	33	10	14	57	8	3	—	11	—	—	—	—		”	”		68
Dec. 20	63	74	2	139	25	8	2	35	2	5	—	7		”	”		181
Dec. 28	15	7	5	27	29	9	5	43	16	2	1	19	3	9	1	13	102
Jan. 6	4	—	1	5	44	5	6	55	22	11	6	39	24	9	5	38	137
Jan. 14	1	1	—	2	2	—	1	3	4	2	3	9	3	5	4	12	26
Jan. 24	1	—	—	1	1	1	1	3	—	—	1	1	8	—	1	9	14
Total 1952/3	180	113	22	316	148	46	15	208	51	20	10	82	38	23	11	72	679
Totals	189	132	24	346	166	149	22	336	63	162	12	238	44	136	13	193	1114

TABLE V

APHIDS TRAPPED 1951/2, 1952/3

LINCOLN 2						DARFIELD 2					
SAMPLING DATE	*M. persicae*	*A. solani*	*M. euphorbiae*	OTHERS	TOTAL	SAMPLING DATE	*M. persicae*	*A. solani*	*M. euphorbiae*	OTHERS	TOTAL
1951/2	1	47	—	36	84	1951/2					
Dec. 16	5	6	—	47	58	Dec. 16		No Sample			
Dec. 23	—	2	—	2	4	Dec. 23	—	54	—	35	89
Dec. 30	—	1	—	7	8	Dec. 30	—	13	—	5	18
Jan. 6	—	—	—	—	—	Jan. 6	—	3	—	—	3
Jan. 14	—	—	—	—	—	Jan. 14	—	—	—	—	—
Jan. 20	—	—	—	—	—	Jan. 20	—	—	—	—	—
Jan. 27	—	—	—	—	—	Jan. 27	—	—	—	—	—
Feb. 3	—	—	—	—	—	Feb. 3	—	—	—	—	—
Feb. 10	—	—	—	—	—	Feb. 10	—	—	—	—	—
Feb. 17	—	—	—	—	—	Feb. 17	—	—	—	—	—
Feb. 27	—	—	—	—	—	Feb. 27	—	—	—	—	—
Mar. 1	—	—	—	—	—	Mar. 1	—	—	—	—	—
Mar. 12	—	—	—	20	20	Mar. 12	—	—	—	29	29
April 1	—	—	—	150	150	April 1	—	—	—	200	200
Total 1951/2	6	56	—	262	324	Total 1951/2	—	70	—	269	339
1952/3						1952/3					
Dec. 5	1	18	—	121	140	Dec. 5		No Sample			
Dec. 12	3	9	—	97	109	Dec. 12		No Sample			
Dec. 20	5	14	—	150	169	Dec. 20		No Sample			
Dec. 28	6	8	—	70	84	Dec. 28		No Sample			
Jan. 6	3	7	3	40	53	Jan. 6	2	8	1	30	41
Jan. 14	2	2	3	15	22	Jan. 14	—	2	—	4	6
Jan. 24	—	—	—	—	—	Jan. 24	—	—	—	—	—
Total 1952/3	20	58	6	493	577	Total 1952/3	2	10	1	34	47
Grand Total	26	114	6	755	901	Grand Total	2	80	1	303	386

TABLE VI

RUNNING OUT OF AUCKLANDER SHORT TOP AND DAKOTAS

HORORATA (Near Darfield)		PREBDLETON (Near Lincoln)	
	% LEAF ROLL		% LEAF ROLL
1944–5	0	1945–6	0
		1946–7	14.7
1947-8	0.75	1948–9	0.1
		1949–0	1.75

AUCKLANDER SHORT TOP

ANNAT (Near Darfield)			SOUTHBRIDGE (Near Lincoln)		
	% LEAF ROLL	% VIRUS Y		% LEAF ROLL	% VIRUS Y
1946–7	0	0	1947–8	0	1
			1948–9	0.4	1.75
			1949–0	0.4	2.7
1949–0	0	0	1950–1	0	0.65
1950–1	0	0	1951–2	0.7	0.25

TABLE VII

WINTER CONDITIONS AT LINCOLN IN 1951 AND 1952

	MIN. TEMP.		DAYS/FROST		HRS. SUNSHINE		RAINFALL INS.		DAYS/RAIN	
	1952	1951	1952	1951	1952	1951	1952	1951	1952	1951
February	51.7	49.7	1	1	6.1	6.6	1.09	6.15	8	8
March	45.3	48.1	3	6	5.5	6.3	1.07	4.21	11	11
April	43.3	46.3	7	5	6.1	3.7	0.83	6.06	13	12
May	37.2	37.7	16	18	4.8	4.2	2.86	3.85	14	12
June	33.2	30.9	19	24	3.6	5.0	1.63	1.92	14	14
July	28.7	25.6	25	21	5.4	4.5	0.88	1.85	12	13
August	37.1	34.0	13	17	3.7	4.7	2.92	1.37	19	16
September	40.2	37.5	9	17	5.8	6.0	2.25	0.46	8	8
October	43.1	41.8	7	4	5.6	5.6	3.42	3.73	12	19
Average	40.1	39.2	11.0	12.5	5.2	5.2	1.88	3.29	12.3	12.5

TABLE VIII

TOTALS/30 LEAVES

	LINCOLN 1		LINCOLN 2		DARFIELD 1		DARFIELD 2	
	1951-2	1952-3	1951-2	1952-3	1951-2	1952-3	1951-2	1952-3
Myzus persicae	9	180	18	148	12	51	6	38
A. solani	19	113	103	46	142	20	113	23
M. euphorbiae	2	22	7	15	2	10	2	11
	30	315	128	209	156	81	121	72

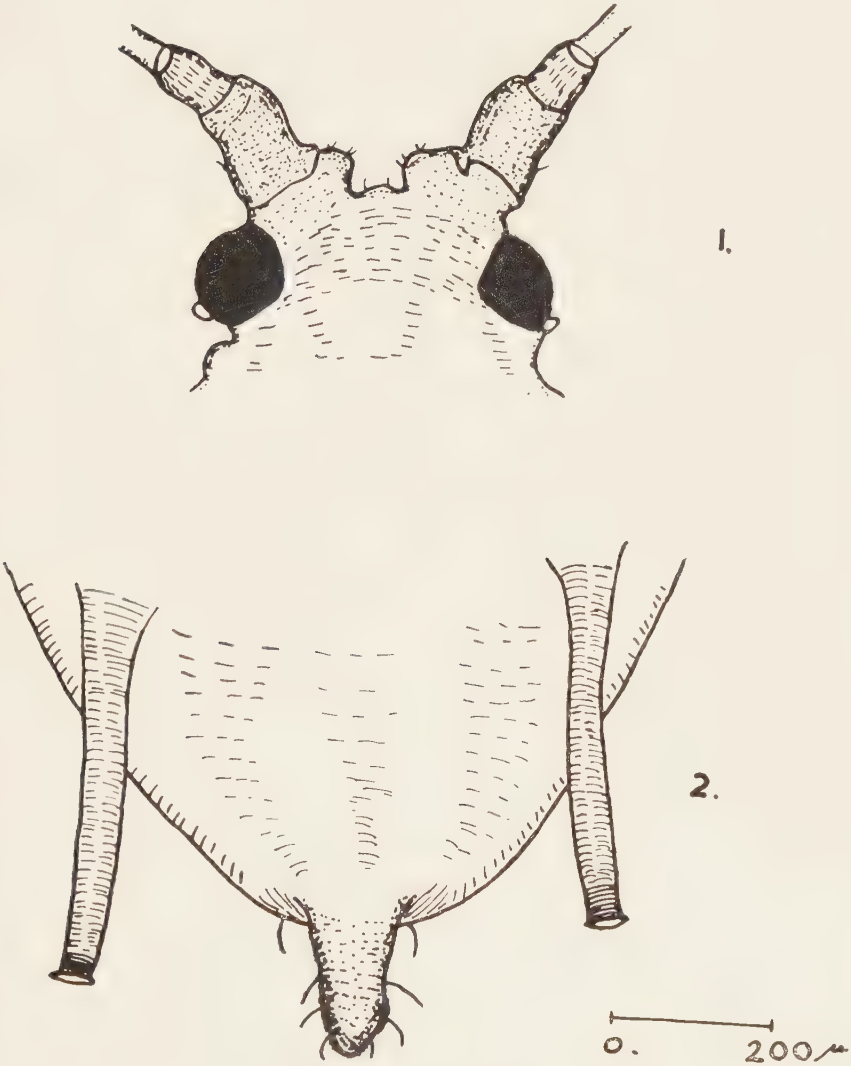


Fig. 1.—*Myzus persicae*
1. Head
2. Cornicles and cauda

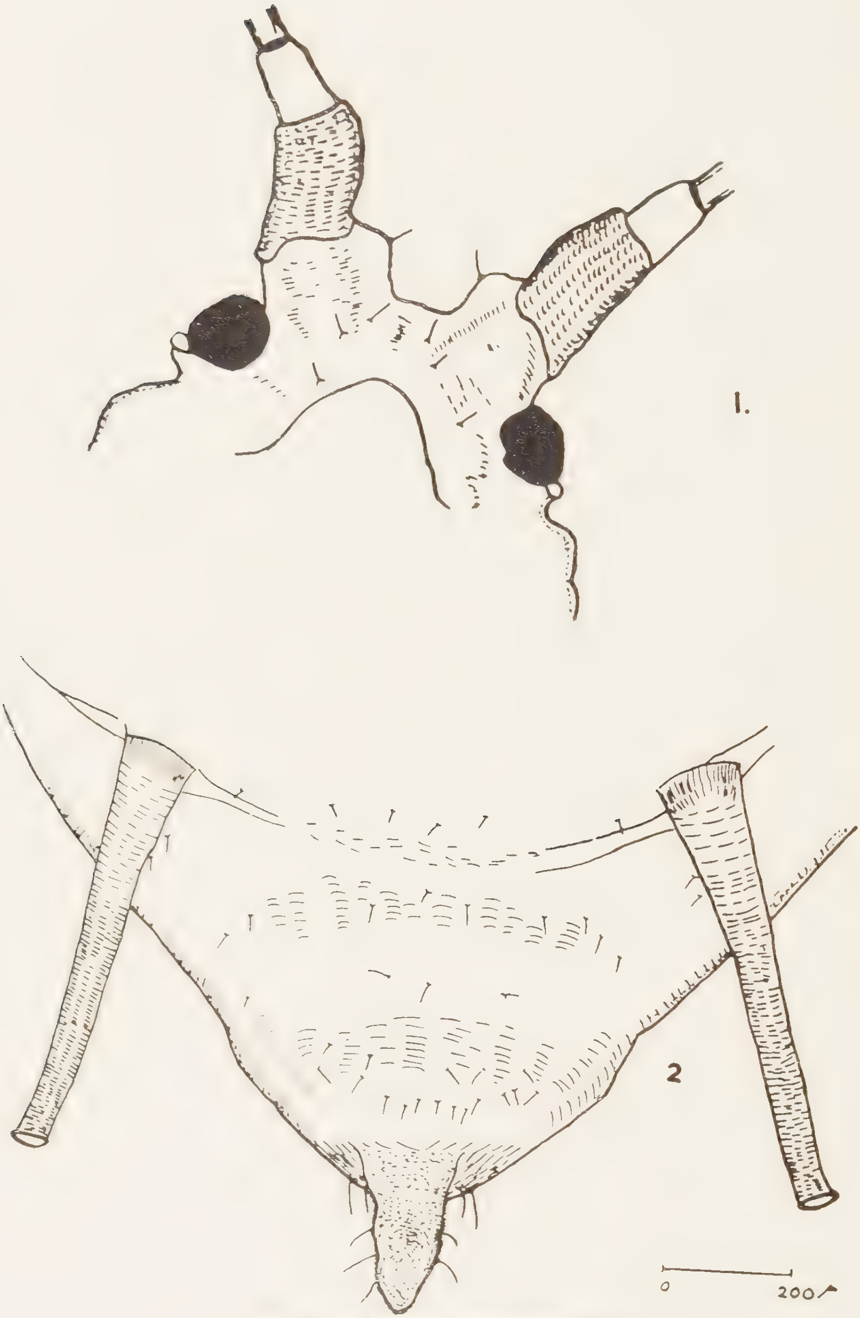


Fig. 2.—A[illegible] Kltb.
1. Head
2. Cornicles and cauda

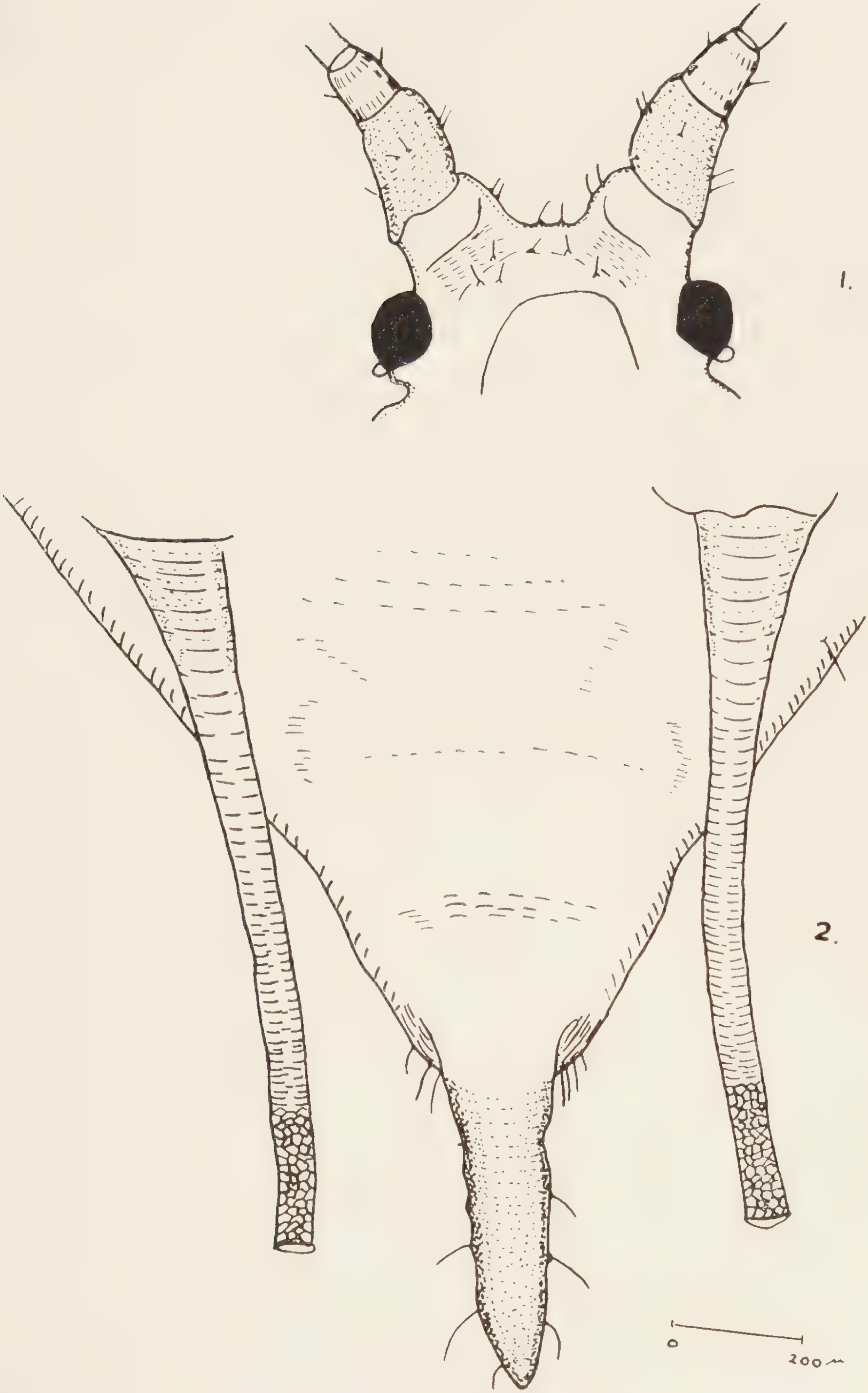


FIG. 3.—*Macrosiphum euphorbiae*
1. Head
2. Cornicles and cauda

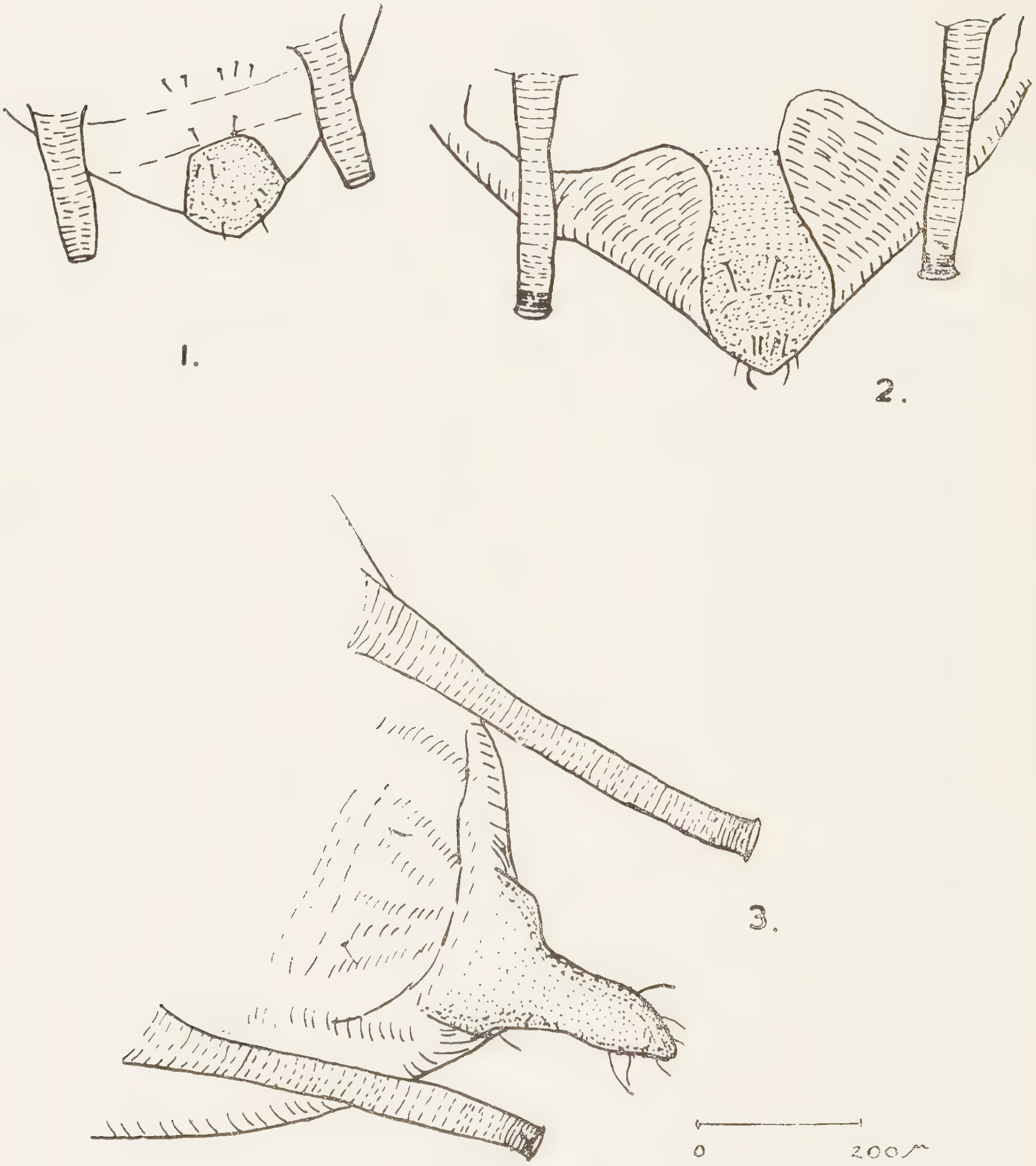


FIG. 4.—Development of cauda
1. Nymph
2. Nymph
3. Adult

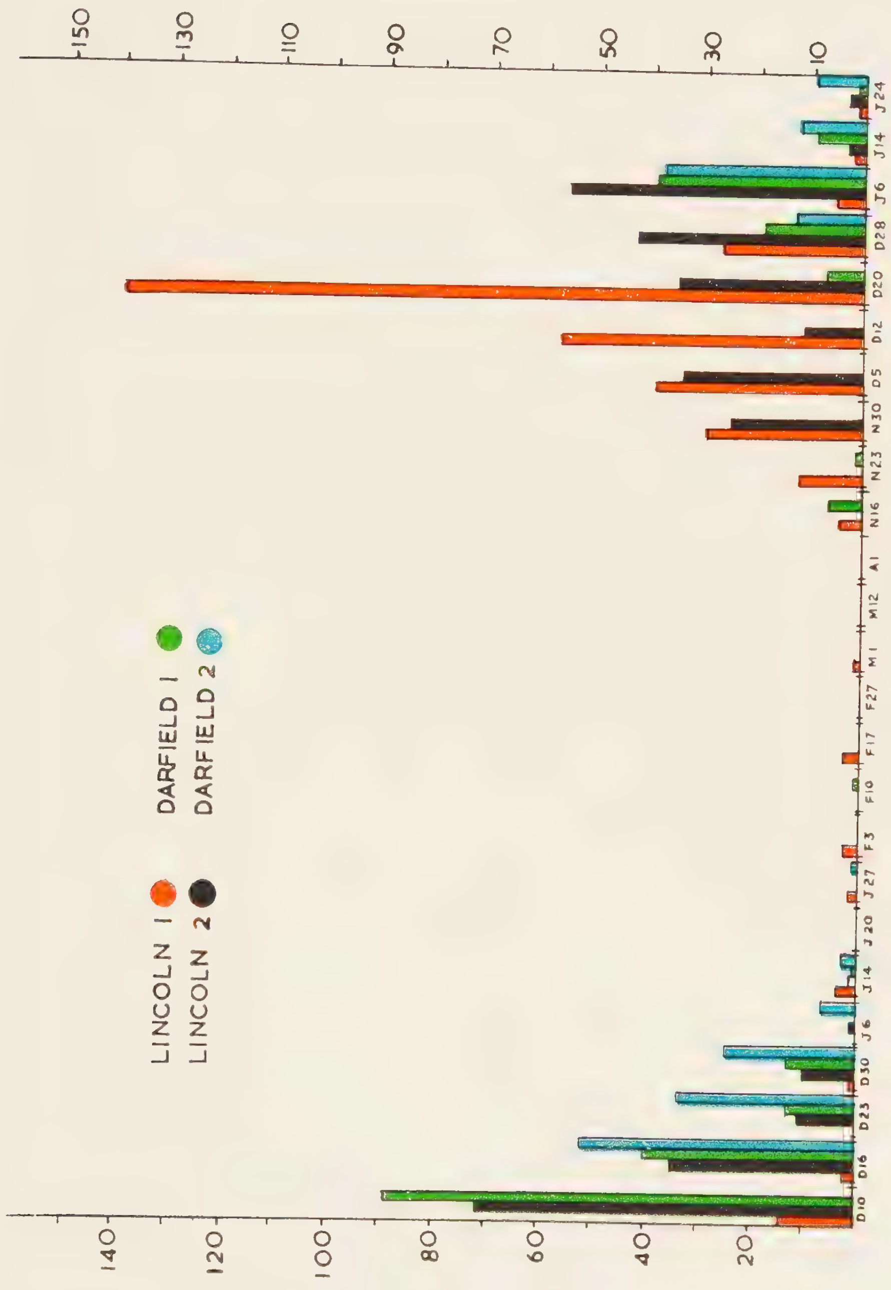


FIG. 5.—Total aphids/30 leaves

November 27, 1953

(Final Divisional Meeting)

Presiding: Dean LEOPOLDO B. UICHANCO, College of Agriculture, University of the Philippines, College, Laguna.

Secretary: Dr. SILVERIO M. CENDAÑA, College of Agriculture, University of the Philippines, College, Laguna.

The Final Divisional Meeting which was to have been held at 2:30 o'clock in the afternoon was cancelled to give opportunity for those in the Zoology Division to participate on the Panel Discussions on Rats and Rat Control with the Divisions of Public Health and Agriculture.

AUTHOR INDEX

Arnow, Ted 919
Ayre, G. L. 1547
Baird, A. B. 1227
Beauchamp, R. S. A. 1105
Bess, Henry A. 1562
Boschma, H. 1495
Britton, E. B. 1383
Brown, Walter C. 1479
Cain, A. J. 1393
Cendaña, S. M. 1347
Cloud, Preston E., Jr. 1009
Coolidge, Harold J. 905
Cooper, L. H. N. 1157
Doty, Maxwell S. 923
Dumbleton, L. J. 1325
Fleming, Richard H. 1177
Fosberg, F. R. 1037
Forest, Jacques 1053
Ganapati, P. N. 1145
Gardner, T. R. 1371, 1475
Given, B. B. 1265
Gressitt, J. Linsley 1319, 1453, 1533, 1539
Haramoto, Frank H. 1275
Hart, T. J. 1165
Herre, Albert W. C. T. 1595
Hiatt, Robert W. 929
Huntsman, A. G. 1123
Jayaraman, R. 1111
Katznelson, H. 1219
King, K. M. 1561
Kondo, Yoshio 1457
Kuronoma, Katsuzo 1089
Kuwayama, Satoru 1251
McLeod, J. H. 1547
Manuel, Canuto G. 1463
Marples, B. J. 1573
Miller, David 1205
Miller R. C. 1575
Monod, Théodore 971
Montalban, Heraclio R. 887
Murthy, V. S. R. 1145
Namocale, P. P. 1347
Newell, Irwin M. 1337
Nishida, Toshiyuki 1562
O'Connor, B. A. 1329
Otanes, Faustino Q. 1413
Pangga, Guillermo A. 1433
Panikkar, N. K. 1111
Pemberton, C. E. 1205
Powell, A. W. B. 1461
Rabanal, Herminio R. 873 887
Ranson, Gilbert 909, 979, 989, 1077
Séguy, E. 1375
Sewell, R. B. Seymour 1139
Sison, Pedro 1299
Spoehr, Alexander 1049
Swingle, H. S. 865
Tanada, Yoshinori 1235
Thorson, Gunnar 1171
Townes, Henry 1546
Tracey, Joshua I., Jr. 907
Turnbull, A. L. 1579
Uichanco, Leopoldo B. 1291
Vaas, K. F. 855
Vachon, Max 1393
Vayssiere, P. 1295
Villadolid, Deogracias V. 853, 873
Watts, B. B. 1621
Wilkinson, A. T. S. 1561
Wimpenny, R. S. 1131
Wood, E. J. Ferguson 1107
Yutuc, L. M. 1511